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ON THE ROLES OF DIRECTED AND RANDOM CHANGES IN GENE FREQUENCY IN THE GENETICS OF POPULATIONS[1]

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INTRODUCTION

Science has largely advanced by the analytic procedure of isolating the effects of single factors in carefully controlled experiments. The task of science is not complete, however, without synthesis: the attempt to interpret natural phenomena in which numerous factors are varying simultaneously. Studies of the genetics of populations, including their evolution, present problems of this sort of the greatest complexity. Many writers on evolution have been inclined to ignore this and discuss the subject as if it were merely a matter of choosing between single factors. My own studies on population genetics have been guided primarily by the belief that a mathematical model must be sought which permits simultaneous consideration of all possible factors. Such a model must be sufficiently simple to permit a rough grasp of the system of interactions as a whole and sufficiently flexible to permit elaboration of aspects of which a more complete account is desired.

On attempting to make such a formulation (Wright, 1931) it was at once apparent that any one of the factors might play the dominating role, at least for a time, under specifiable conditions, but it was concluded that in the long run "evolution as a process of cumulative change depends on a proper balance of the conditions which at each level of organization—gene, chromosome, cell, individual, local race—make for genetic homogeneity or genetic heterogeneity of the species."

The purpose of the present paper is to reiterate this point of view in connection with certain misapprehensions which have arisen and in particular to analyze certain data which have been presented recently by R. A. Fisher and E. B. Ford (1947) as invalidating what they consider my point of view. This discussion leads to mathematical comparisons between the amount of random drifting of gene frequency expected in small populations merely from accidents of sampling and that expected in large ones from variations in degree and direction of selection or in amount and character of immigration.

SMALLNESS OF POPULATION SIZE AS A FACTOR

In spite of his repeated emphasis on dynamic equilibrium among all factors as the most favorable condition for

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evolution, the author has often been credited with advocating the all importance of a single factor, viz. sampling effects in very small populations. Thus in Goldschmidt's stimulating book "The Material Basis of Evolution" (1940) he states: "The adherents of such a view" (NeoDarwinism) "derive much comfort from the results of population mathematics, especially Wright's calculation (1931) showing that small isolated groups have the greatest chance of accumulating mutants even without favorable selection. . . . It is the contention that small isolated populations have the greatest chances from the standpoint of population mathematics." What I actually stated on this matter in the summary of the paper referred to was as follows: "In too small a population there is nearly complete fixation, little variation, little effect of selection and thus a static condition, modified occasionally by chance fixation of rare mutations, leading inevitably to degeneration and extinction." The same conclusion has been reiterated in all more recent general discussions.

Population Structure as a Factor

This misapprehension may have arisen from the emphasis put on population structure later in the same summary: "Finally in a large population, divided and subdivided into partially isolated local races of small size, there is a continually shifting differentiation among the latter, intensified by local differences in selection, but occurring under uniform and static conditions, which inevitably brings about an indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species" (than in a comparably large, random breeding population). It should be noted that a favorable population structure, under this view, may be prevented by excessive density of population, as well as by too small a total number (cf. Wright, 1943). The implied relation of size of population to rate of evolution is not a simple one. I suspect that "inevitably" is too strong a word as used above, but otherwise this quotation still represents my position on the importance of population structure in evolution. The ways in which it is important were, of course, brought out more completely elsewhere in this paper and have been developed further in later papers.

This leads to consideration of a recent inaccurate statement of my views by R. A. Fisher and E. B. Ford. Their first reference is in the main an acceptable statement of the role which I have attributed to random shifts in gene frequencies, provided that the word "partially" is inserted before "isolated" and it is clearly understood that the primary significance of the process is as one of a number of adjuncts to intergroup selection. "Great evolutionary importance has been attached by Sewall Wright (1931, 1932, 1935, 1940) to the fact that small shifts in the gene ratios of all segregating factors will occur from generation to generation owing to the errors of random sampling in the process by which the gametes available in any one generation are chosen to constitute the next. Such chance deviations will, of course, be greater the smaller the isolated population concerned. Wright believes that such nonadaptive changes in gene ratio may serve an evolutionary purpose by permitting the occurrence of genotypes harmoniously adapted to their environment in ways not yet explored and so of opening up new evolutionary possibilities."

The next sentence indicates, however, that the authors have wholly missed the major point stressed in all of the cited papers. "Consequently he claims that subdivision into isolated groups of small size is favorable to evolutionary progress not as others have held through the variety of environmental conditions to which such colonies are exposed but even if the environment were the same for all, through nonadaptive and casual changes favored by small population

size." Actually the point stressed most in these papers was the simultaneous treatment of all factors by the inclusion of coefficients measuring the effects of all of them on gene frequency in a single formula. Thus in the 1931 paper the formula for distribution of gene frequencies in a partially isolated local population included the coefficient N_1 for effective size of the local population, s_1 for selection due to local conditions, m_1 for rate of immigration and q_m for gene frequency among the immigrants (mutation pressure was here assumed to be the same throughout the species). This simultaneous treatment made it possible to specify the conditions under which one or another process would dominate with respect to a particular gene. Sampling fluctuations were treated as only one of a number of processes which lead to trial and error among local populations (Wright, 1931, p. 151). This has been reiterated in all later discussions. Thus in the 1940 paper (p. 175) it was noted that "in a large population, subdivided into numerous partially isolated groups, both adaptive and nonadaptive differentiation is to be expected" and it was concluded that conditions are most favorable for evolution when both processes are occurring. The 1935 paper dealt with quantitative variability, due to multiple factors, with the optimum near the mean. The principal conclusion was that slight oscillations in the position of the optimum in local populations provide an important mechanism by which all gene combinations with approximately the same effect in respect to the character under consideration come to be tried out with respect to secondary effects. It was recognized that such oscillations must be of considerable period to be important. Some significance in causing random changes in gene frequency had, however, been attributed to short time oscillations in severity of selection (Wright, 1931) but this effect was not then analyzed mathematically. This question will be taken up later in this paper.

Fisher and Ford continue with an analysis of annual fluctuations of the frequency of a certain gene in an isolated population of the moth *Panaxia dominula*. They decide that the fluctuations are too great to have been due to accidents of sampling and hence conclude that they must have been due to fluctuations in the action of selection. They arrive at the following generalization.

"The conclusion that natural populations in general, like that to which this study is devoted, are affected by selective action, varying from time to time in direction and intensity and of sufficient magnitude to cause fluctuating variations in all gene frequencies is in good accordance with other studies of observable frequencies in wild populations. We do not think, however, that it has been sufficiently emphasized that this fact is fatal to the theory which ascribes particular evolutionary importance to such fluctuations in gene ratios as may occur by chance in very small isolated populations. . . . Thus our analysis, the first in which the relative parts played by random survival and selection in a wild population can be tested, does not support the view that chance fluctuations can be of any significance in evolution."

Thus Fisher and Ford insist on an either-or antithesis according to which one must either hold that the fluctuations of *all* gene frequencies that are of any evolutionary significance are due to accidents of sampling (attributed to me) or that they are *all* due to differences in selection, which they adopt. As already noted, I have consistently rejected this antithesis and have consistently accepted both sorts as playing important, complementary, and interacting roles. According to the criteria developed in the 1931 paper and later, the genes in a population may be put into 3 classes with respect to the roles of selection and random sampling. One class of segre-

gating genes in any population may be expected to be almost wholly dominated by selection in one way or another, another class almost wholly by accidents of sampling, while an intermediate class, to which special importance was attributed, will show important joint effects.

Fluctuations in Gene Frequency in Panaxia dominula

To which of these classes the particular gene studied by Fisher and Ford belongs makes no difference from this standpoint. The use of criteria may, however, be illustrated by further analysis of the data.

A highly isolated population of the moth *Panaxia dominula* near Oxford, England, was studied. A rather conspicuous color variety, *medionigra*, has been present in this colony for at least 20 years but has not been found elsewhere. A more extreme variety, *bimacula*, which occurs in this colony much less frequently has been shown to be the homozygote. The frequency of the medionigra gene is indicated by study of all available collections to have been less than 1.2% before 1929. The frequency had risen to 9.2% by 1939 when careful study was begun and reached its peak 11.1% in 1940. It dropped to 6.8% next year and since then has varied between 4.3% and 6.5%, without any well defined trend. From 1941 to 1946, the total number of imagines that emerge each season has been estimated from the proportions of captured and marked moths, recaptured after release. The most important data and estimates are shown in table I.

The authors make a statistical analysis of the data for the years 1939 to 1946 on the assumption that there are 1000 parents of each generation. They find that the chance that such great fluctuations could arise from accidents of sampling on this basis is less than 1% ($\chi^2 = 20.806$, 7 degrees of freedom, 1% value 18.475). They conclude that fluctuations in the action of natural selec-

Table I

	Estimates of Population Size N	Types of moth collected				q_m Frequency of m	δq_m Shift in q_m
		+/+	+/m	m/m	Total moths		
Up to 1928	—	164	4	—	168	.012	
							(+.080)
1939	—	184	37	2	223	.092	
							+.019
1940	—	92	24	1	117	.111	
							−.043
1941	2000–2500	400	59	2	461	.068	
							−.014
1942	1200–2000	183	22	—	205	.054	
							+.002
1943	1000	239	30	—	269	.056	
							−.011
1944	5000–6000	452	43	1	496	.045	
							+.020
1945	4000	326	44	2	372	.065	
							−.022
1946	6000–8000	905	78	3	986	.043	
							—

Estimated population size (N), numbers of each genotype and total moths captured, frequency (q_m) of medionigra gene (m) and shift in frequency (δq_m) to next generation (at least 11 generations in first case).

tion must therefore have been responsible for them.

In making these calculations, two years are included in which there are no estimates of population size. If the collections for the 6 years, 1941–1946, for which such estimates were made, are tested merely for heterogeneity, we find that χ^2 is 11.8 which, with 5 degrees of freedom, indicates a probability of about .04 that accidents of sampling, based merely on the limited size of the collections, could have given rise to as large deviations from the average. Thus there is no very compelling reason from the fluctuations themselves for assuming that there were any real fluctuations at all, during this period. It is necessary to include the two earlier years to get convincing evidence for real fluctuations. If this is done, χ^2 rises to 35.9, which, with 7 degrees of freedom, is far beyond even the 0.1% value, 24.3, leaving no doubt of the reality of a shift in gene frequency. The big shift is that between these two earlier years as a group (av. 9.8%) and the following 6 years (5.2%) for which the difference is 4.9 times its standard error, with a probability of about 10^{-6} of arising from accidents of sampling. The question thus largely resolves into what happened between summer 1940 and the next summer to cause such a marked drop in gene frequency and what happened at some undetermined time or times between 1928 when gene frequency was only 1.2% in collections and 1939 to cause a rise to 9.2%.

These changes may well have been due to shifts in the conditions of selection as supposed by the authors but there is nothing in the data as presented to rule out the alternative possibility of reduction to an exceptionally small effective population number on two (or more) occasions, an interpretation for such fluctuations that has long been urged by Elton. Nothing is stated of population size in the period 1928–1939 and all that is stated of the year 1940 is that the moths were not as common in this or later years as in 1939. The number actually collected in 1940 (117) was much less than in any other year.

The mean square of the 7 apparent shifts in gene frequency from 1939 to 1946 is .000488. The mean variance to be expected merely from the sizes of the samples collected is .000269. The difference, .000219, is an estimate of the variance of real shifts in gene frequency in the population.

The authors give no estimate of the amount of variation in selective value necessary to account for such fluctuations. Assume for mathematical simplicity that the heterozygote is intermediate between the two homozygotes. It may be noted that it makes no appreciable difference for this purpose what assumption is made about the rare homozygote bimacula. Assume that selective value is independent of gene frequency and has no trend but varies according to nonsecular fluctuations in conditions from year to year.

If medionigra has a selective advantage of s over type in a particular year, bimacula of $2s$, gene frequency tends to shift by the amount $\delta q = sq(1 - q)$.[2] The estimate for the variance of such shifts is thus $\sigma^2_{\delta q} = \sigma_s^2 \Sigma q^2(1 - q)^2/n$, using σ_s^2 for the variance of fluctuations in the value of the selection coefficient s and n for the number of years used in calculating an average. For the 7 observed shifts in gene frequency, $\sigma^2_{\delta q} = .00453\sigma_s^2$. On equating this to the estimate of the real fluctuations (.000219) we find $\sigma_s^2 = .0483$, $\sigma_s = .22$. It is to be noted that this means an absolute standard deviation of 22%, not a mere 22% of the value of s (which in fact is here assumed to have an average value of zero). A standard deviation of .22 means that in the course of half a century the selective value of medionigra heterozygotes would vary between semilethality (or semisterility) ($s = -.50$) to a 50% advantage over type ($s = +.50$).

[2] See Appendix.

The homozygotes, on the hypothesis adopted, would range from complete lethality (or sterility) to a selective value twice that of type. This last aspect, however, is quite certainly not tenable since bimacula appeared as regularly when gene frequency dropped as when it rose. Its frequency in the total data was, as the authors note, very close to what would be expected in the absence of selection (11 observed, 10.2 expected).

It seems very probable that the heterozygotes actually have a slight net advantage over both homozygotes, as suggested by the authors. The major shifts in frequency are however so much greater than the possible systematic shifts that the latter can be ignored for the present purpose.

It is of interest to see how small the effective size of population (N) would have to have been to account in full for the estimated real variance of fluctuations. The variance for one generation is $q(1 - q)/2N$. For the period of years in question, we take $\overline{q(1 - q)}/2N = .0648/2N$ as the mean variance to be expected from this cause. On equating to the estimated variance of real fluctuations, .000219, we find $N = 150$.

The effective size of population over a succession of generations is the harmonic mean of the effective sizes for the separate ones and thus may be very much smaller than the arithmetic mean. Its value is largely dominated by occasional very small values in particular years, if these occur. We come back to the conclusion that if the effective number of parents of the 1941 moths was very small (some 100 or less) it is possible to account for all fluctuations as those of small populations, even though the effective number from 1941 to 1946 were as much as 1000.

However, 117 moths were actually captured in the summer of 1940. The question of the relation between effective and apparent population size requires further consideration.

The harmonic mean of the authors' estimates of total number of imagines per year from 1941 is about 2000. The females are stated to lay some 200–300 eggs each. Thus the total number of eggs is typically more than 200,000. The females are described as not flying after emergence until they have laid a considerable proportion of their eggs, probably within the first 24 hours after fertilization. Thus the broods are largely concentrated in single spots, subject to the same environmental vicissitudes. The larvae are stated to winter in the 3rd instar. It is estimated that there may be over 50,000 well grown larvae in the spring to be reduced typically to a thousand or a few thousands by the time of emergence of the adults. The greatest menace to the late larvae is considered to be virus disease and to the pupae, mice.

The authors tacitly assume that this elimination of more than 99% of the individuals from egg to imago is random with respect to broods, unless some allowance is intended by using 1000 instead of 2000 as the population number in their calculations. The possibility of a much greater discrepancy between apparent and effective population number is a matter that would seem to require investigation. Thus analyses of some dozen pure breeds of live stock, including cattle, horses, sheep and swine by means of the inbreeding coefficient of hypothetical progeny from random parents (McPhee and Wright, 1925; Lush, 1943), have shown that in each the effective population number is of the order of 100 or at most a few hundred, a very small proportion of the total numbers registered per generation (tens of thousands in most cases). The special reasons responsible for the extreme smallness of N in these cases would not hold in nature. It is not, however, safe to assume without investigation that there are not other reasons for a considerable reduction of N. If, in the present case, there are any conditions of weather or disease that tend to destroy whole broods at any time in the annual cycle, the effective population number would

be cut down accordingly. Again recent work by Dobzhansky and associates (1942, 1944) has revealed an extraordinary prevalence of segregating factors in *Drosophila pseudoobscura* in nature with high selection coefficients under some or all environmental conditions. At first sight this would seem to strengthen the view that selective differences are so important that fluctuations due to limitation in the number of parents would be negligible. This is certainly true for the genes or chromosome conditions in question but very heavy selective elimination in such respects would bring about a correlation between brood mates in fate and so automatically lower the effective population number for other more neutral segregating factors. In a sense, the ensuing shifts in the frequencies of these could be attributed to selection, but if the shifts in these neutral genes are equally likely to occur in either direction they must be credited to sampling variability. The situation is similar, except for the element of intent, to one that is familiar to livestock breeders. With very intensive selection for particular characters, others must be allowed to vary at random if numbers are to be maintained (cf. Wriedt, 1930). It would seem possible, a priori, that the causes of coincident elimination of broodmates (common environment, and common highly selective heredity) may be as important as causes of random elimination. If the former should produce an effect equivalent to elimination of 90% of the broods while the latter are causing random elimination of 90% within the favored broods, leaving the observed 1% to carry on, the effective population number would be only 10% of the apparent number and easily capable of accounting for the observed annual fluctuations.

The alternative is the hypothesis that variety medionigra had an average selective advantage of about 20% from 1928 to 1940 whatever fluctuations there may have been, and then shifted to approximate semisterility or semilethality in that year, followed by fluctuations without trend thereafter.

The present author is certainly in no position to decide between these hypotheses (or some combination of them). In a recent study of the frequency of lethals in nature in one of the chromosomes of *Drosophila pseudoobscura*, it was found that these were only about one fourth as numerous as they should have been on the basis of the adequately determined mutation rate and the necessary rate of elimination as recessive lethals in a large random breeding population (Wright, Dobzhansky and Hovanitz, 1942). On introducing all factors, that might shift gene frequency, into equations describing the observed results it appeared that the discrepancy could be accounted for either by a slight selection against heterozygotes (coefficient s) or by a slight excess tendency toward brother-sister mating (average inbreeding coefficient F) or a combination. In fact the coefficients entered the equation together (to the first order) as the sum ($s + F = .018$) so that it was impossible to separate them. Direct tests for selection (not included in the above statement) indicated no significant selection but the required amount was so slight that more extensive tests would have been necessary. This indeterminacy was unfortunate but it seems likely that more progress will be made in analyzing the difficult problems of the genetics of natural populations if all possibilities are treated symmetrically and any indeterminacy is brought clearly into view rather than concealed by an approach from the point of view of advocacy of any single factor, even one of such undoubted importance as selection.

Comparison of Diverse Type of Fluctuations

It is noted above that the observed annual fluctuations in the frequency of medionigra could be due to fluctuations in selective value above and below zero with a standard deviation of .22. Even

if this is the correct interpretation for this gene, it does not follow that all segregating genes show comparable fluctuations. Genes with an average frequency of .05 in an indefinitely large population, and with no net selective advantage or disadvantage ($\bar{s} = 0$) but with fluctuations in selective value measured by a standard deviation $\sigma_s = .10$, would vary in gene frequency to about the same extent as would genes with the same average frequency but with no fluctuations in degree of selection in a population of effective size 1000. In the former case, $\sigma_{\delta q} = \sigma_s q(1-q)$ approximately, by the formula given earlier. With the values given above, $\sigma_{\delta q} = .10 \times .05 \times .95 = .0048$. In the case of neutral genes in a population of 1000, $\sigma_{\delta q} = \sqrt{q(1-q)/2N} = \sqrt{.05 \times .95/2000} = .0049$.

If this sort of calculation is applied to genes with frequency .50, it would appear that fluctuating selective values with standard deviation of only .02 would be equivalent to the effect of sampling in a population of 1000. This, however, does not allow for the fact that the new values of gene frequency with q larger or smaller than .50, that result from the fluctuations, are subject to greater subsequent fluctuations from sampling than from selection, because of the relatively slow falling off of the term $\sqrt{q(1-q)}$ in comparison with $q(1-q)$ as q deviates from .50. A more thorough analysis of the effects of the two kinds of fluctuation is necessary.

In the long run, random fluctuations in gene frequency, whatever their cause, tend to result in a certain distribution of gene frequencies ($\varphi(q)$) about whatever equilibrium value ($\hat{q}$) is determined by the systematic pressures (Δq). The formula of these distribution curves may be found (see appendix). Figures 1 to 7 show such curves (formulae in appendix) under various postulated conditions. The abscissas are the possible gene frequencies from 0 to 1. The ordinates are the frequencies with which

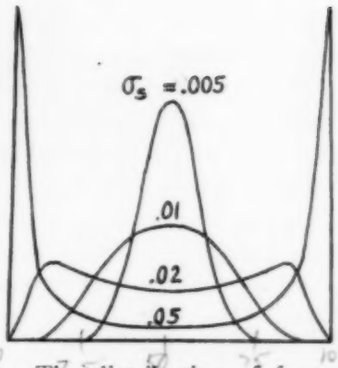

FIG. 1. The distribution of frequencies for genes with different amounts of random fluctuation of selection pressure ($\sigma_s = .005, .01, .02, .05$) in a population in which the only systematic pressure is that due to immigration ($\bar{s} = 0$, $m = .0001$) directed to a mean $\hat{q} = .50$. Size of population is assumed to be so great ($N > 10^6$) that fluctuations of gene frequency due to sampling are negligible.

these values may be expected to occur in the long run if the conditions remain the same. In figures 1 and 2 it is assumed that the frequency of a gene in a local population always tends to move toward .50 because of immigration from the rest of the species, in which this is the average gene frequency. The rate is assumed to be $m = .0001$ (one out of every 10,000 individuals in each generation has become a member of the population by immigration). In figure 1 the population is assumed to be very large, but gene frequency fluctuates about .50

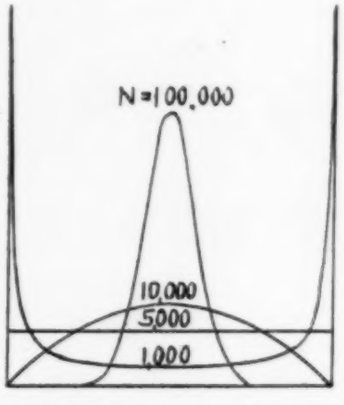

FIG. 2. The distribution of gene frequencies in small populations ($N = 1000$, 5000, 10,000, 100,000) in which the only systematic pressure is the same as in figure 1 ($\bar{s} = 0$, $m = .0001$, $q_I = .50$) but the only random changes in gene frequency are those due to sampling.

because of variations in the direction and severity of selection (mean selective differential zero ($\bar{s} = 0$), but standard deviation, σ_s, taking values .005, .01, .02 and .05 in the cases illustrated). The value $\sigma_s = .005$ means that the selective value of the heterozygote relative to type ranges from about 99% to 101% of type (deviations of about $2\sigma_s$ in each direction from 100%) and that the homozygotes have twice this range. In this case, the immigration pressure toward gene frequency .50 practically restricts gene frequency to the range .25 to .75. In the last case, however, the cumulative effects of the relatively violent fluctuations in selective value ($\sigma_s = .05$) keep the gene close to fixation or loss most of the time in spite of the continual return of both alleles by immigration. These curves may be compared with those in figure 2 in which no selective differentials are assumed at any time but the effective size of population is assumed to be so small (N = 100,000, 10,000, 5,000 or 1,000 in the 4 cases illustrated) that the cumulative effects of accidents of sampling cause random drift about gene frequency .50, in spite of continual pressure toward this value from the immigration.

It may be seen that a standard deviation of .005 in selective value of heterozygotes (twice this in homozygotes) in a population of millions is only slightly more effective than mere accidents of sampling in a population of 100,000. A standard deviation of .01 in a population of millions is less effective than sampling in a population of 10,000. A standard deviation of .05 is roughly equivalent to sampling in a population of 1000. This is considerably greater than the value .02 reached by comparisons at $q = .50$.

If the immigration pressure were 10 times as great ($m = .001$) the same distribution curves would be obtained with values of σ_s that are 3.2 times as great and with values of N one-tenth as great. In the case of fluctuations in selection the form of the curve depends merely on the value of the parameter m/σ_s^2 and in the case of sampling drift on the value of Nm.

It may be noted that even if m is as great as .01, the variations of gene frequency with $\sigma_s = .05$ in a very large population are only slightly greater than those due to sampling in a population of effective size 1000 (same distributions as those shown for $\sigma_s = .005$ in figure 1 and N = 100,000 in figure 2 with m assumed to be .0001 in both cases). Thus Fisher and Ford's contention that variations in the direction and intensity of selection cause much greater fluctuations in the frequencies of *all* genes than does sampling amounts to the contention that all segregating genes in a population such as that studied are subject to fluctuations in selective value with standard deviations much greater than .05.

Figures 3, 4 and 5 describe the situation where selection tends to increase gene frequency ($\bar{s} = .0002$) while this is opposed by immigration (rate $\bar{m} = .0001$) from populations which lack the gene. In figure 3 it is supposed that fluctuations are due wholly to ones in selective value. It requires a standard deviation

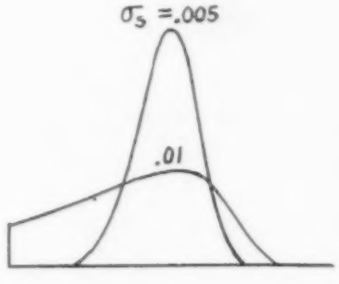

FIG. 3. The distribution of frequencies for genes with different amounts of random fluctuation of selection pressure ($\sigma_s = .005, .01$) where there is pressure of favorable selection $\bar{s} = .0002$ in heterozygotes, twice this in homozygotes, opposed by pressure of immigration ($m = .0001$) from populations in which the gene is absent ($q_I = 0$). Size of population is assumed to be so great ($N > 10^6$) that fluctuations of gene frequency due to sampling are negligible. Mutational origin at a very low rate is required to prevent permanent loss of the gene if $\sigma_s = .01$.

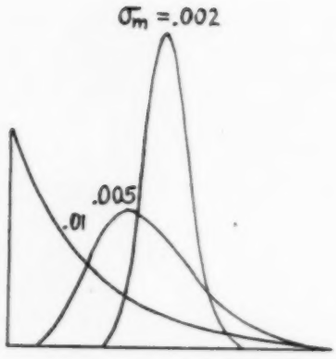

FIG. 4. The distribution of frequencies for genes where the systematic pressures are the same as in figure 3 ($\bar{s}$ = .0002, no dominance, $\bar{m}$ = .0001, q_I = 0) but the amount of immigration fluctuates to different extents (σ_m = .002, .005, .01) and all other random fluctuations are negligible. Mutational origin at a very low rate is required to prevent permanent loss of the gene if σ_m = .01.

approaching σ_s = .005 to cause much departure from equilibrium ($\bar{q}$ = .50). With σ_s = .01 there is wide departure in the direction of low frequencies and with still larger σ_s, the fluctuations in selective values tend to bring about complete and permanent loss of the gene under the postulated conditions. Figure 4 shows distribution of gene frequencies due to fluctuation in immigration rate (a factor which has no effect of this sort where immigration is responsible for the only systematic pressure as in figures 1 and 2). The standard deviation must again be relatively enormous (σ_m = .002, where

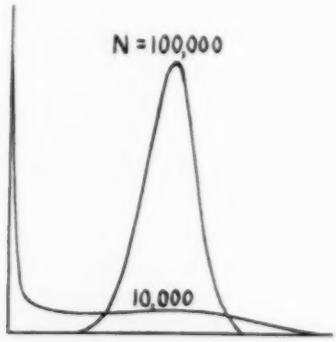

FIG. 5. The distribution of gene frequencies in populations of 10,000 and 100,000 where the systematic pressures are the same as in figures 3 and 4 (s = .0002, no dominance, m = .0001, q_I = 0) except that mutation at the rate $v = 10^{-6}$ is assumed to prevent permanent loss. Random fluctuations of frequency are assumed to be due wholly to sampling.

$\bar{m}$ = .0001) to cause much cumulative effect. There is a much greater effect and a lowering of mean gene frequency if σ_m = .005 and loss of the gene becomes inevitable if σ_m exceeds .01. It may be shown that fluctuations in the gene frequency of immigrants are even less effective. Figure 5 permits comparison with the effects of small population size, under like conditions, except that in this case it is assumed that complete loss is prevented by mutation at the rate of 10^{-6} per generation (s = .0002, m = .0001, v = .000001). It may be seen that the effect of sampling in a population of 100,000 is roughly comparable to that of fluctuation of selective value σ_s = .005 or of fluctuation in the amount of immigration σ_m = .002. In a population of 10,000 the gene would inevitably be lost unless restored by mutation. Even under the assumed conditions, the gene would be completely absent more than 50% of the time in this case.

It seems probable that there are many genes, especially those involved in quantitative variability, that have low net selective values ($\bar{s}$ less than .001 and even than .0001) and correspondingly small fluctuations in value. Fisher indeed has urged that an important phenomenon, the prevalence of dominance of type over deleterious major mutations, is due to genes that act solely as modifiers of dominance, the *maximum* selection pressure on which according to his calculation (Fisher, 1928, 1930) is of the same order as the mutation rate of the mutant gene in question, and thus of the order 10^{-6} per generation. While I have had qualms about accepting the existence of a large class of such nearly neutral genes (Wright, 1929a, b, 1934) [3]

[3] The efficacy of selection in modifying dominance where the heterozygote is the direct object of selection (a subject to which Fisher has devoted much attention (Fisher, 1935; Fisher and Holt, 1944)) does not require the existence of a class of genes with maximum selective differentials anything like as small as 10^{-6} and was explicitly accepted in my first discussion of this matter.

I have nevertheless been inclined to adopt the view that most evolutionary change is due to changes in frequencies of genes of the sorts of which Harland wrote "the modifiers really constitute the species." The "isoalleles" of Stern and Schaeffer (1943) belong in this category.

While annual fluctuations in selective value can have little significance with respect to such factors, variations in selective value of longer period (such as the writer had in mind in his 1935 paper) are, of course, more important. Still more important are the relations between net pressures on genes over very long periods and the effects of sampling. According to the criteria given in the 1931 paper, sampling variance is significant only when the net pressures are small. This is illustrated by changing the interpretations of figures 2 and 5 along the lines indicated earlier. On multiplication of the net pressures due to selection, immigration and mutation by any factor, the distribution curve for gene frequencies remains the same if the hypothetical size of population is divided by the same factor. Immigration pressure is not necessarily the same for all genes but is the same on the simplest model. Selection pressure (and mutation pressure) may, however, differ enormously among different genes and thus may put these in different classes with respect to the importance of sampling. Figure 6 deals with the case of genes which tend to persist at 50% frequency because of equal selection against both homozygotes and which are prevented from ever being permanently lost by mutation rates of 10^{-6} per generation in both directions. Effective population size is taken as 10,000. If the selective advantage of the heterozygote is 1% ($s = .01$), or more, there is very little variation of gene frequency about the equilibrium frequency, .50. If, however, the advantage is only 0.1% there is rather wide variation. Genes for which $\bar{s} = .0003$ vary in frequency from one extreme to the other and each homozygote is fixed about 18% of the time. For genes for which $s = .0001$, each homozygote is fixed more than 30% of the time and frequencies between 10% and 90% are rare in spite of the pressure toward 50% due to both selection and mutation. Without the latter, indeed, one or the other phase would soon become permanently fixed even with genes for which $s = .0003$. It has sometimes

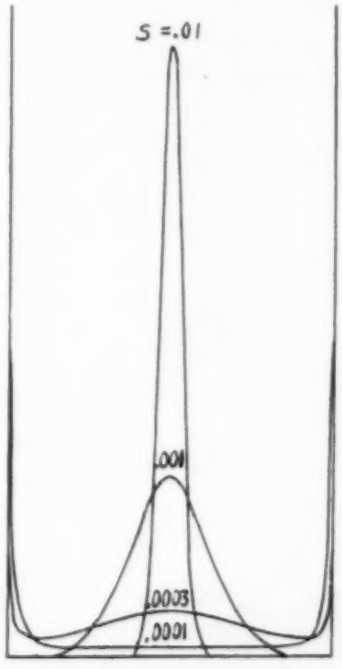

FIG. 6. The distributions of frequencies of 4 classes of genes in a population of effective size 10,000. Selection is assumed to favor the heterozygotes equally over both homozygotes but to different extents ($s = .01, .001, .0003, .0001$) in the 4 classes. Low rates of mutation equal in both directions ($v = u = 10^{-6}$) are assumed to prevent complete fixation of either homozygote.

been held that nonadaptive differentiation due to sampling can only occur in populations of a few hundred (cf. Lack, 1947) but given enough time and sufficiently neutral segregating genes, this can occur in completely isolated populations whenever $4Nv$ is less than 1, v being the mutation rate from the allele most likely to be fixed under the conditions. Thus with mutation rates of 10^{-6}, there can be random fixation up to a population size of 250,000.

Figure 7 deals with a more complex situation in a population of 10,000. Immigration at rate $m = .0001$, tending to establish a gene frequency of .10, is here supposed to be supplemented by selection in which the heterozygous mutant has advantages ranging from .00001 to .001 and homozygotes twice as much in each case. Those genes for which $s = .001$ are almost fixed by selection in spite of the adverse immigration pressure. Genes for which $s = .0001$ are, on the other hand, largely dominated by the immigration pressure but their frequencies vary over a wide range. At certain intermediate values (e.g. $s = .0002$) there are peak frequencies both above and below 50%. Genes for which $s = 10^{-5}$ are so much dominated by the sampling effect that their frequencies are below 0.5% more than 20% of the time and below 5% about half the time in spite of the pressure of immigration toward a gene frequency of 10% and of selection toward complete fixation.

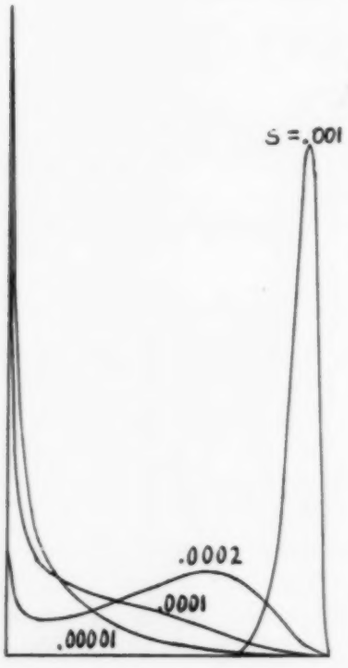

FIG. 7. The distributions of frequencies of 4 classes of genes in a population of effective size 10,000 as in figure 6. In this case, selection is assumed to favor the genes to different extents in the 4 classes ($s = .001, .0002, .0001, .00001$) with no dominance, but with opposition by immigration ($m = .0001$) from population in which gene frequency q_I is .10.

The importance of random fluctuations of gene frequency, whatever their cause, cannot be adequately evaluated by considering single pairs of alleles in a single population. What is important is simultaneous variation of gene frequencies at many loci, each with many alleles which differ only slightly in selective value, in each of many local populations. The significance is in contributing to the material for the selection of genetic systems as wholes, which may be expected to take place through the welling up of population growth and emigration from those centers in which at the moment the most adaptive systems happen to have been arrived at and the modification by immigration of those centers in which population growth has become relatively depressed because of less successful general adaptation.

It must be emphasized again that this contribution of random differentiation of local population with respect to the more neutral sets of alleles is only one aspect of the whole trial and error process. The great importance of the contribution of selective differentiation among such populations with respect to less neutral alleles is obvious. Moreover, the nonadaptive differentiation is obviously significant only as it ultimately creates adaptive differences.

SUMMARY

Evolution is a process in which many diverse factors are acting simultaneously. Mathematical treatment requires simultaneous treatment of all determinate factors, including both the systematic pressures (recurrent mutation, immigration and selection), which are wholly determinate in principle, and the cumulative effects of random fluctuations of gene frequencies, of which only the variance is determinate. Any one of the factors may play the dominating

role for a time under specifiable conditions.

Conditions are held to be most favorable for a continuing process where there are certain states of dynamic equilibrium at many loci. This situation is found to the greatest degree in a population in which there is sufficient isolation of many local centers of population growth and emigration to provide the condition for continual trial and error. The "errors" are the relatively indeterminate elements in the situation: novel mutations at the gene level, and the effects of accidents of sampling, and of variations in the local conditions of selection and migration at the level of the local population. The "trials" are the orderly reactions of the species to changes of gene frequencies, due to more determinate factors, of which selection dominates in the long run. Where there are important secular changes in external relations, selection pressure dominates the situation almost completely until a new state of approximate adjustment is reached and trial and error processes again take over.

The reiteration of the above viewpoint has been stimulated by certain misinterpretations which have arisen. Several authors have attributed to the author the view that accidents of sampling constitute the most important evolutionary process and that conditions are more favorable for evolution the smaller the total population. This is a view that has been emphatically rejected from the first.

Especial attention is devoted to a somewhat different misinterpretation in a recent paper by R. A. Fisher and E. B. Ford. They hold that fluctuations of gene frequencies of evolutionary significance must be supposed to be due wholly either to variations in selection (which they accept) or to accidents of sampling. This antithesis is to be rejected. The fluctuations of some genes are undoubtedly governed largely by violently shifting conditions of selection but for others in the same populations, accidents of sampling should be much more important and for still others both may play significant roles. It is a question of the relative values of certain coefficients.

An analysis of fluctuations in the frequency of a certain gene in a population of the moth *Panaxia dominula*, observed by Fisher and Ford and used by them as the basis for their generalizations, raises considerable doubt as to which category this particular gene belongs.

A comparison is made between the distribution of gene frequencies due to the cumulative effects of various types of random fluctuation in the presence of various pressures. Such comparisons support the view that random drift due to sampling in small local populations is an important member of this category and thus a factor of which account must be taken where there is a favorable type of population structure.

Appendix

The distribution of gene frequencies under diverse causes of fluctuation

The factors of evolution may best be brought under a common viewpoint by measuring each by the change which it tends to bring about in each generation in the gene (or chromosome) frequency (q) under consideration. They may be classified conveniently according to the degree of determinacy in their effects.

The term "pressure" has been used figuratively (Wright, 1929, 1931) for all evolutionary factors with recurrent directed effects capable at least in principle of precise mathematical formulation. The symbol Δq is used. The pressures of recurrent mutation and immigration have linear effects on gene frequency. They can introduce a gene into populations in which it has been absent. Selection pressure can be defined sufficiently broadly to include all processes (such as differential mortality, differen-

tial fecundity, differential emigration) which tend to change gene frequency systematically without either change of the hereditary material itself (mutation) or introduction from without (immigration). Selection pressure is necessarily zero either if $q = 0$ or $q = 1$ in contrast with mutation and immigration pressures.

Random fluctuations in gene frequency may be due to accidents of sampling or to fluctuations in the values of the coefficients involved in the evolutionary pressures. The symbol δq has been used for such a change. Direction is indeterminate but the variance ($\sigma^2_{\delta q}$) can be specified at least in principle.

In addition it seems necessary to recognize a category that is indeterminate both in direction and variance. This includes events that are unique or nearly so in the history of the species: nonrecurrent mutations, unique hybridizations, nonrecurrent selective events, unique extreme reduction in numbers, etc. The distinction between recurrent events and ones so rarely recurrent as to require treatment as indeterminate is, of course, an arbitrary one.

The systematic pressures (Δq) may lead to fixation or loss of a gene. If not, they tend to hold its frequency at a certain equilibrium point (or points): any value of q at which $\Delta q = 0$, provided that this is stable (Δq opposite in sign to $(q - \hat{q})$ where $\hat{q}$ is the equilibrium value). The random fluctuations (δq) tend to cause random drift from an equilibrium point. The resultant is a probability distribution $\varphi(q)$ which exhibits the frequencies with which the frequency of the gene in question takes all values between 0 and 1 in the long run. It is also the distribution of frequencies of this gene at any moment among a number of populations all subject to the same conditions. The formula for $\varphi(q)$ is a relatively simple function of Δq and $\sigma^2_{\delta q}$ (Wright, 1938).

$$\varphi(q) = (C/\sigma^2_{\delta q})e^{2\int(\Delta q/\sigma^2_{\delta q})dq},$$

where C is a constant such that

$$\int_0^1 \varphi(q)dq = 1.$$

Figures 1 to 7 are obtained by substituting various values of Δq and $\sigma^2_{\delta q}$ in this formula. Consider first, however, a somewhat more general case in which heterozygous mutants have a selective advantage s, homozygous mutants an advantage of $2s$ and immigration displaces the proportion m in each generation by immigrants with gene frequency q_I. We must distinguish the mean values of these coefficients ($\bar{s}$, $\bar{m}$, $\bar{q}_I$) and their standard deviation σ_s, σ_m and σ_{q_I}, if they are subject to fluctuation. For small values of $\bar{s}$:

$$\Delta q = \bar{s}q(1 - q) - \bar{m}(q - \bar{q}_I).$$

Mutation pressure may be introduced by taking advantage of the equivalence of the theories of immigration pressure and mutation pressure. Letting $\bar{v}$ be the mean rate of mutation to the gene and $\bar{u}$ that from it per generation

$$\begin{aligned}\Delta q &= \bar{s}q(1-q) + (\bar{v} + \bar{m}\bar{q}_I)(1-q) \\ &\quad - [\bar{u} + \bar{m}(1-\bar{q}_I)]q \\ &= \bar{s}q(1-q) - (\bar{m} + \bar{u} + \bar{v}) \\ &\quad \times [q - (\bar{v} + \bar{m}\bar{q}_I)/(\bar{m} + \bar{u} + \bar{v})].\end{aligned}$$

For simplicity in most of what follows, $\bar{m}$ will be used in place of $(\bar{m} + \bar{u} + \bar{v})$ and $\bar{q}_I$ in place of $(\bar{v} + \bar{m}\bar{q}_I)/(\bar{m} + \bar{u} + \bar{v})$.

As indicated above random fluctuations in gene frequency may be due to fluctuations in selection (σ_s), in amount of immigration (σ_m), or in gene frequency of immigrants (σ_{q_I}) as well as to accidents of sampling, and in general are due to some combination of all of these. We wish, however, to compare their separate effects.

(a) Fluctuations only in selection

$$\begin{aligned}\delta q &= (s - \bar{s})q(1-q) \\ \sigma^2_{\delta q} &= \sigma_s^2 q^2 (1-q)^2 \\ \varphi(q) &= C[q/(1-q)]^{2[\bar{s} - m(1-2q_I)]/\sigma_s^2} \\ &\quad \times q^{-2}(1-q)^{-2} e^{-2m[q_I(1-q) + (1-q_I)q]/\sigma_s^2 q(1-q)}\end{aligned}$$

(b) Fluctuations only in amount of immigration

$$\delta q = -(m-\bar{m})(q-q_I)$$
$$\sigma^2_{\delta q} = \sigma_m{}^2(q-q_I)^2$$
$$\varphi(q) = C(q-q_I)^{2[s(1-2q_I)-\bar{m}-\sigma_m{}^2]/\sigma_m{}^2} \times e^{-2s[(q-q_I)^2+q_I(1-q_I)]/\sigma_m{}^2(q-q_I)}$$

(c) Fluctuations only in gene frequency of immigrants

$$\delta q = m[q_I - \bar{q}_I]$$
$$\sigma^2_{\delta q} = m^2\sigma^2_{q_I}$$
$$\varphi(q) = Ce^{[6m\bar{q}_I q - 3q^2(m-s) - 2sq^3]/3m^2\sigma^2 q_I}$$

(d) Fluctuations only from sampling (Wright, 1931)

$$\sigma^2_{\delta q} = q(1-q)/2N$$
$$\varphi(q) = Ce^{4Nsq}q^{4Nmq_I-1}(1-q)^{4Nm(1-q_I)-1}$$

Figures (1) and (2) deal with the special case of genes for which the only pressure is that due to immigration ($m = .0001$) and gene frequency in the immigrants is .50.

Fig. 1

$$\Delta q = -m(q-.5)$$
$$\sigma^2_{\delta q} = \sigma_s{}^2q^2(1-q)^2$$
$$\varphi(q) = Cq^{-2}(1-q)^{-2}e^{-m/\sigma_s{}^2q(1-q)}$$

Fig. 2

$$\sigma^2_{\delta q} = q(1-q)/2N$$
$$\varphi(q) = C[q(1-q)]^{2Nm-1}$$

Figures 3, 4 and 5 relate to cases in which the pressure of favorable selection ($\bar{s} = .0002$) with no dominance is opposed by the pressure of immigration ($m = .0001, q_I = 0$). Mutational origin of the gene at a low rate is required to prevent its loss in extreme cases. In figure 5 this rate is taken as $v = 10^{-6}$.

Fig. 3

$$\Delta q = \bar{s}q(1-q) - mq$$
$$\sigma^2_{\delta q} = \sigma_s{}^2q^2(1-q)^2$$
$$\varphi(q) = C[q/(1-q)]^{2(\bar{s}-m)/\sigma_s{}^2} \cdot \times q^{-2}(1-q)^{-2}e^{-2m/\sigma_s{}^2(1-q)}$$

Fig. 4

$$\sigma^2_{\delta q} = \sigma_m{}^2q^2$$
$$\varphi(q) = Cq^{2(s-\bar{m}-\sigma_m{}^2)/\sigma_m{}^2}e^{-2sq/\sigma_m{}^2}$$

Fig. 5

$$\Delta q = sq(1-q) - mq + v(1-q)$$
$$\sigma^2_{\delta q} = q(1-q)/2N$$
$$\varphi(q) = Ce^{4Nsq}q^{4Nv-1}(1-q)^{4Nm-1}$$

Figures 6 and 7 make comparisons between genes subject to different degrees of selection in a population of limited size ($N = 10{,}000$). In figure 6 it is assumed that selection favors heterozygotes equally over both homozygotes but varies in degree ($s = .01, .001, .0003$ or $.0001$).

Low rates of mutation, equal in both directions ($u = v = 10^{-6}$), are assumed to prevent permanent fixation.

Fig. 6

$$\Delta q = -[2v + 2sq(1-q)][q-.5]$$
$$\sigma^2_{\delta q} = q(1-q)/2N$$
$$\varphi(q) = Ce^{4Nsq(1-q)}q^{4Nv-1}(1-q)^{4Nv-1}$$
$$= Ce^{40{,}000sq(1-q)}[q(1-q)]^{-.96}.$$

In figure 7, it is assumed that immigration at rate $m = .0001$ tends to maintain gene frequency at $q_I = .10$ but that this is disturbed to varying extents by favorable selection (no dominance). $s = 10^{-5}$, 10^{-4}, 2×10^{-4} and 10^{-3} respectively in a population of 10,000.

Fig. 7

$$\Delta q = sq(1-q) - m(q-q_I)$$
$$\sigma^2_{\delta q} = q(1-q)/2N$$
$$\varphi(q) = Ce^{4Nsq}q^{4Nmq_I-1}(1-q)^{4Nm(1-q_I)-1}$$
$$= Ce^{40{,}000sq}q^{-.6}(1-q)^{2.6}$$

The frequencies in fixed classes in any of these cases are estimated where necessary from the subterminal classes by formulae (Wright, 1931)

$$f(0) = [f(1/2N)]/4N(mq_I+v),$$
$$f(1) = \{f[(2N-1)/2N]\} /4N[m(1-q_I)+u],$$

where

$$f(q) = \varphi(q)/2N.$$

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AN ALTITUDINAL TRANSECT OF DROSOPHILA ROBUSTA STURTEVANT

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INTRODUCTION

Both in plants (see for instance Clausen, Keck and Hiesey, 1940) and in animals it is well known that orderly clines may occur within populations of a species which covers any considerable altitudinal range on mountain-sides. The successive waves of genetically different ecological types which replace each other up the side of a mountain may or may not be distinct enough to be considered subspecies taxonomically. Thus the clines may appear to be smooth or roughly stepwise in form.

In animals altitudinal clines are well known in birds. Rand (1936) has described changes with altitude in New Guinea birds and finds that in 17 of 60 species studied the forms from the higher altitudes are either larger (more commonly) or darker (rarely) than the lowland forms. In only two cases were the reverse changes found. Here in many species the changes with altitude were so gradual that subspecies could not be recognized with certainty.

In insects Hovanitz (1941) has made a study of variation in the coloration of butterflies and its correlation with the environment. In some species he finds clear altitudinal clines, but in many instances the clines are obscured by the complications of the micro-environment to which the species is adapted. Since most of the variations in wild Lepidoptera that have been tested have been found to be inherited, he concludes that the observed clines are based on variations in the genotype rather than on direct response to the environment.

Dobzhansky (1943, 1948) has shown that populations of *Drosophila pseudoobscura* and *D. persimilis* living at different altitudes in the mountains of California may differ in the frequency of certain gene arrangements. In several cases, the change with elevation is gradual, so that the phenomenon is best described as an altitudinal cline.

In *Drosophila robusta,* Carson and Stalker (1947) and Stalker and Carson (1947) have shown that north-south geographic clines exist both for frequencies of various chromosome inversions and for various morphological characteristics. Since the morphological characteristics were measured on flies reared under standard laboratory conditions, they must have been based on genetic differences between the geographic strains.

If northern and southern strains of the same species have characteristic morphological and chromosomal properties, then it might be expected that within a population inhabiting a mountain-side similar morphological and chromosomal clines might occur, with the northern types found at higher altitudes where the ecological conditions more nearly approached those in the north.

It is the purpose of this paper to report a study of such a mountain-side population conducted with a view to determining the differences associated with changes in altitude, and to determine further whether or not these differences parallel those which differentiate northern and southern strains of the species.

MATERIALS AND METHODS

The collections on which the present study are based were made from July 9–15, 1947, in the vicinity of Gatlinburg, Tennessee. Eight trapping locations were selected between the Forney Ridge Park-

ing Area (elevation: 6310 feet) in the Great Smoky Mountains National Park, and a bridge over the West Fork of the Little Pigeon River approximately ten miles north of Gatlinburg by automobile (elevation: 1000 feet). At the higher elevations, traps were set in dense woods in the general vicinity of roadside altitude markers within the Park. *D. robusta* was not captured at the 5000 and 6000 foot levels; the data given herein are, therefore, based on collections from the six locations extending from the 4000 foot level to the valley. The altitudes of the three lower stations and the linear distances given were determined from topographic maps. Each location was visited approximately twice daily.

The following descriptions characterize the general features of the habitat at each collecting location.

4000 feet. Dense, moist hemlock and yellow birch forest—the principal undergrowth consisted of *Rhododendron maximum.* This is approximately 500 feet below typical spruce-fir Canadian Zone associations. Although a large number of traps at this location were destroyed by bears, a sufficiently large collection of various species of Drosophila was made to permit the statement that *D. robusta* is uncommon at this level.

3000 feet. The major flora consisted of tulip tree, locust, hickory, persimmon and sugar maple. Distance from the 4000 foot location: 3.5 miles.

2000 feet. Deciduous forest similar to the preceding, including also red maple and dogwood, with a heavy undergrowth of Japanese honeysuckle and jewel-weed. Distance from the 3000 foot location: 2.5 miles.

1400 feet. Forest along the edge of the West Fork of the Little Pigeon River, consisting primarily of red oak, sweet gum, American holly, sycamore and tulip tree. There was a considerable undergrowth of poison ivy. Distance from the 2000 foot location: 4.0 miles. This location was outside the Park, 1.0 miles by automobile north of the Gatlinburg city limits.

1200 feet. Flora similar to the preceding, but including some *Rhododendron maximum* and wild grape; traps were set in underbrush adjacent to the Little Pigeon River. Distance from the 1400 foot location: 3.5 miles.

1000 feet. Dense deciduous woods of locust, elm and sycamore; the undergrowth was heavily carpeted with Japanese honeysuckle. The location was adjacent to the Little Pigeon River. Distance from the 1200 foot location: 4.5 miles.

The entire transect has a lineal extent of approximately 18 miles and includes an overall declination of 3000 feet. A diagrammatic representation is given in the upper part of figure 1.

The general biology of *Drosophila robusta*, methods of collection, rearing and measuring have been discussed elsewhere (Carson and Stalker, 1947; Stalker and Carson, 1947). In the present study cy-

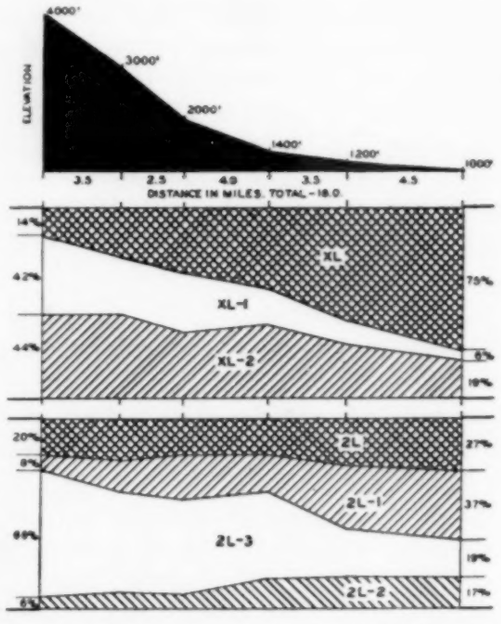

FIG. 1. Diagram of the altitudinal transect (in black) near Gatlinburg, Tennessee (elevation: 1400 feet) and the frequency changes for the gene arrangements in the left arm of the X chromosome (upper diagram) and the left arm of the second chromosome (lower diagram) of *Drosophila robusta.* The frequency of each arrangement at 4000 feet is given at the left; at 1000 feet, at the right.

TABLE 1. *Gametic frequencies in per cent of the gene arrangements in chromosomes 2 and 3 of* Drosophila robusta *near Gatlinburg, Tennessee*

Altitude in feet	*n*	Chromosome 2						Chromosome 3	
		Left arm				Right arm		Right arm	
		2L	2L-1	2L-2	2L-3	2R	2R-1	3R	3R-1
4000	74	20.3	8.1	5.4	66.2	91.9	8.1	21.6	78.4
3000	102	22.5	15.7	7.8	54.0	85.3	14.7	22.5	77.5
2000	301	18.6	23.6	7.0	50.8	88.7	11.3	19.9	80.1
1400	278	19.4	19.8	15.5	45.3	91.7	8.3	25.2	74.8
1200	127	24.4	33.9	15.7	26.0	89.8	10.2	28.3	71.7
1000	145	26.9	37.3	17.2	18.6	86.9	13.1	33.8	66.2

tological data are from F_1 larvae obtained either through matings of wild males to females which are carriers of known gene sequences; or from wild females, already inseminated when captured or mated to wild males from the same locality. Adult F_1 males and females from wild-caught flies were aged at 25.5° C. and then allowed to produce an F_2 generation which was then reared for measurement. All measurements reported here were made on adult, thoroughly hardened females. Measurements made with the aid of an ocular micrometer and are expressed as the original micrometer readings. The measurement "1.00" in the tables would correspond to an absolute size of 720 micra.

CYTOLOGICAL OBSERVATIONS

The frequencies of the gene arrangements present in the population of Gatlinburg and vicinity at the six altitudes are given in tables 1 and 2. Examination of these data reveals a number of changes with decreasing altitude, especially in the left arm of the X chromosome and the left arm of the second chromosome (see also fig. 1). The increase in frequency of XL and the decrease of 2L-3 are gradual and progressive as one descends the mountain. The increase of XL is primarily at the expense of XL-1 at higher altitudes; in the valley, both XL-1 and XL-2 decline. 2L-3 decreases gradually and is replaced in the population by increases in frequency of the other three arrangements in this arm.

In the right arm of the X (table 2) some irregularity is displayed; there is, however, a clear increase of XR at the expense of XR-2 in the valley. A somewhat comparable change, although more orderly, occurs in the right arm of the third chromosome. Here (table 1) it is evident that although 3R is unchanged at the higher localities, the valley populations (1400, 1200 and 1000 feet) show

TABLE 2. *Gametic frequencies in per cent of the gene arrangements in the left and right arms of chromosome X of* Drosophila robusta *near Gatlinburg, Tennessee*

Altitude in feet	*n*	Left arm			Right arm		
		XL	XL-1	XL-2	XR	XR-1	XR-2
4000	43	13.9	41.9	44.2	16.3	0.0	83.7
3000	66	25.8	40.9	33.3	28.8	0 0	71.2
2000	245	33.5	31.8	34.7	26.1	0.0	73.9
1400	277	42.6	19.5	37.9	17.0	0.3	82.7
1200	106	57.5	13.2	29.3	38.7	0.0	61.3
1000	116	75.0	6.0	19.0	44.0	0.9	55.1

a progressive increase for this arrangement. The right arm of the second chromosome is alone in showing little or no change in the area studied.

XR-1 is the only arrangement present in very small numbers. This arrangement is characteristic of populations of the middle west; reaching its highest frequency in Iowa (Carson and Stalker, 1947). It was previously unknown from the Gatlinburg area, which must nearly constitute its southeastern limits.

Discussion

Despite the fact that distinct clinal changes occur in frequencies of gene arrangements on the mountainside and extending down into the valley, an important fact is immediately apparent; these clines are by no means simple recapitulations of the north-south geographical clines known to exist in this species (Carson and Stalker, 1947). 2R and 3R, for instance, are both most frequent in the northern United States. Both show gradual declines in frequency as one goes south. 3R, in fact, is completely replaced by its alternative, 3R-1, south of the southern boundary of Tennessee. This boundary, however, is only known to be valid at low elevations in the western part of the state. The situation may be different in the mountainous east. Neither of these arrangements shows parallel clines on the mountainside; 2R is unchanged over the Gatlinburg transect, whereas 3R shows a definite reverse tendency, being more frequent in valley than at higher elevations.

Differences in the karyotypic constitution of populations from different areas have been interpreted as reflections of fundamental adaptations of the species to different ecological conditions. If this is true, the lack of full correspondence between geographical and altitudinal gene arrangement frequencies is not surprising. Two facts especially should be taken into consideration. In the first place, it would be absurd to consider the higher altitudes in the Smoky Mountains as ecologically equivalent to any northern area in the United States at a lower elevation. Some floral associations and, of course, certain aspects of temperature may be similar, but other, probably equally important features, such as humidity, rainfall and daily temperature range, to mention only a few, may be widely different. Secondly, Dobzhansky (unpublished data, cited in 1948 paper) has shown by population cage experiments with *Drosophila pseudoobscura* that the same gene arrangement from different geographic localities may have a different selective value and hence different gene contents. In line with this, it may be noted that the gene arrangement Arrowhead in *D. pseudoobscura* shows no change with altitude on Mt. San Jacinto in California, whereas Chiricahua does (Dobzhansky, 1943). Three hundred miles to the north in the Sierras, however, the situation is reversed; Arrowhead shows a cline with altitude and Chiricahua is approximately unchanged. To return to *D. robusta*, 3R at 4000 feet in the mountains of Tennessee, for example, may not necessarily have gene contents identical to the same arrangement in central Iowa. Under such circumstances, the absence or reversal of a cline is readily understandable.

The considerations above obviously do not exclude the possibility that the arrangement contents and the environment may be sufficiently similar in two separated geographical areas so that arrangement frequencies in one area are similar to, or approximate, those in the other. This, in fact, seems to be the situation with respect to 2L-3 and XL-1 (fig. 1). Both of these arrangements are typically northern in distribution. Gatlinburg, Tennessee, is the southernmost locality at which either has been found; they are unknown in the extensive collections to the southwest of this area (Carson and Stalker, 1947). The occurrence of these arrangements at Gatlinburg did not seem consistent with their northern distributions over the rest of the range of the species and this was one of the peculiarities which prompted the present investigation. This

phenomenon is now readily explained. Both show their highest frequencies at the highest altitudes, declining sharply as one goes down into the valley. These declines are so sharp (2L-3: 66% to 19%; XL-1: 42% to 6%) as to suggest that neither extends very far from the mountains. Both arrangements are commonly found in the northeast, and it is tempting to suggest that their geographical distribution to the south may be confined largely to the southward extension of the Appalachian Mountains.

Dobzhansky (1948) has demonstrated altitudinal clines for some of the gene arrangements in the 3rd chromosomes of *D. pseudoobscura* and *D. persimilis* in the Sierra Nevada Mountains of California. The transect studied was approximately 60 miles in extent and covered an altitudinal range of 8000 to 9000 feet. The data have been interpreted as indicating that the various levels of these clines represent ecotypes in which natural selection maintains frequency equilibria for certain gene arrangements. In *D. pseudoobscura* it has been shown that these equilibria may be shifted seasonally. As neither species is found at elevations below the foothills (Jacksonville), these ecotypes could be considered local differentiations, within a single large mountain population, to the extremely diverse ecological conditions.

The Gatlinburg transect of *D. robusta*, on the other hand, is much smaller; its extent is about eighteen miles and it represents a declination of only 3000 feet. Despite this, the changes in frequencies in *D. robusta* over this transect are much sharper and more striking than those found in *D. pseudoobscura* and *D. persimilis*. Furthermore, it is interesting to note that the steepness of the Gatlinburg clines is not positively correlated with the steepness of altitude changes. In fact, the changes in the valley, where there is a declination of only 400 feet, are in all cases as sharp or sharper than higher on the mountain. A measure of the ecological similarity of two areas is difficult to make, especially for a species whose breeding habits are largely unknown, but the conclusion is inescapable that the ecological differences between the three lower stations are not as great as the differences between the three upper stations. Unlike *D. pseudoobscura* and *D. persimilis*, *D. robusta* ranges away from the mountains into the lowlands to the west, leading one to the conclusion that a possibly large, low-level population exists adjacent to the mountains.

Rather than suggesting that the sharp clines found in *D. robusta* reflect similar clines in ecological conditions, these facts seem to indicate that there are two general populations in the Gatlinburg area, a mountain and a low-level population. Each of these populations might have its own principal ecotype (expressed by frequency equilibria for certain gene arrangements). These ecotypes could be conceived of as being confluent over a relatively narrow area, presumably repre-

TABLE 3. *Locality means for five basic measurements and Discriminants D_2 and D_3 at six different altitudes in Great Smoky Mountains*

Altitude in feet	Number flies	Number strains	Thorax length	Head width	Femur length	Wing length	Wing width	Discriminant	
								D_2*	D_3*
4000	140	4	2.139	1.723	1.088	3.218	2.148	5.501	0.698
3000	306	14	2.149	1.722	1.094	3.208	2.146	5.494	0.709
2000	359	36	2.144	1.723	1.086	3.196	2.142	5.448	0.694
1400	394	43	2.131	1.718	1.073	3.149	2.101	5.297	0.670
1200	150	15	2.142	1.724	1.074	3.135	2.108	5.271	0.666
1000	160	16	2.139	1.717	1.079	3.144	2.108	5.317	0.681

* See text.

sented in this case by the valley of the West Fork of the Little Pigeon River. Such a situation would result in steep clines which would not necessarily reflect stepwise adaptations.

Morphological Observations

Table 3 gives the mean measurements for each of the five basic characters from each of the six localities sampled. The second and third columns of the table indicate the number of strains and F_2 females on which each mean is based. Approximately equal numbers of females were measured in each strain from any one locality.

Figure 2 shows diagrammatically the changes with altitude of the mean locality measurements. In this figure the locality means are shown as percentages of the unweighted mean for the whole mountain sample. Thus, in the case of thorax length, the locality mean at 4000 feet (2.139) is 99.92% of the over-all mean thorax-length (2.1407). At 3000 feet the locality mean of 2.149 is 100.39% of the over-all mean, etc. By using these percentages rather than the raw means, the very considerable interlocality differences in large dimensions, such as wing-length, are more directly comparable to the differences in small dimensions such as head-width and femur-length.

Table 4 summarizes the tests of significance of the inter-locality and inter-regional differences shown diagrammatically in figure 2. All tests of significance were made on the raw data rather than on the percentage transformations. By a comparison of figure 2 and table 3 it will be noted that

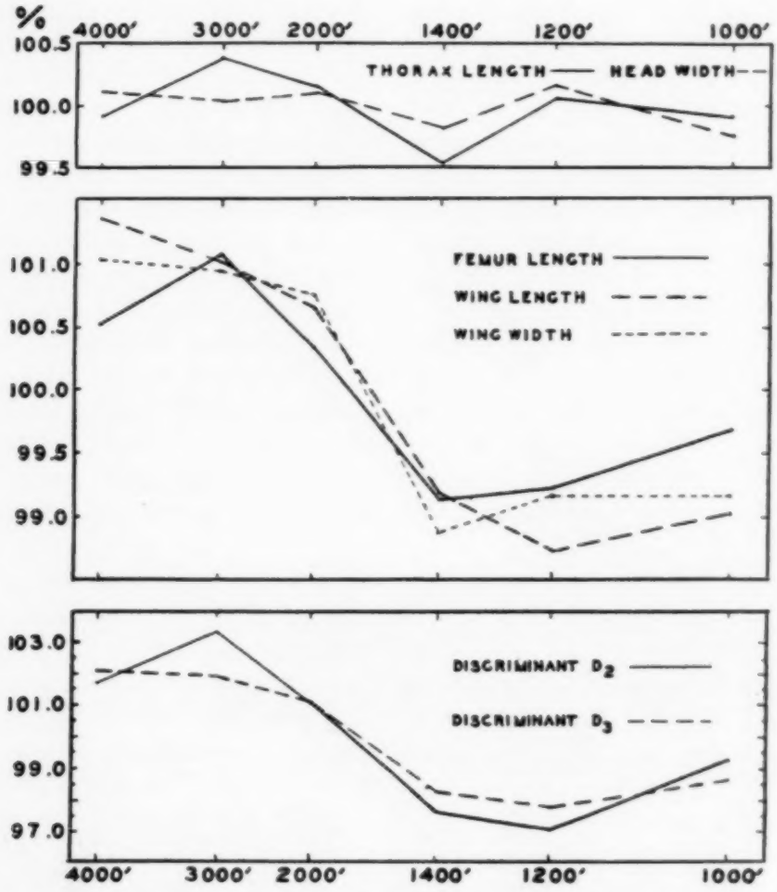

Fig. 2. Changes with altitude of five basic characters and Discriminant Functions D_2 and D_3. Each character or Discriminant is expressed as per cent of the unweighted mean of the six locality means.

TABLE 4. *Summary of tests of significance*

The results of the tests are expressed as variance ratios. The variance ratios at the 5% and 1% levels of significance are given at the right of each section of the table; the upper figure representing that ratio at the 5% limit in each case.

Localities and regions compared	Variance ratios					Variance ratios at 5% and 1% levels	Variance ratios		Variance ratios at 5% and 1% levels
	Thorax length	Head width	Femur length	Wing length	Wing width		Discriminant D_3	Discriminant D_2	
All six	2.215	0.785	9.690**	13.243**	12.545**	2.29 3.17	12.420**	5.632**	1.96 2.58
4000′ 3000′	0.950	0.032	1.010	0.269	0.055	4.49 8.53	0.011	0.390	3.11 5.06
1200′ 1000′	0.110	2.452	1.042	0.596	0.016	4.18 7.60	0.360	0.484	2.60 3.86
4000′ 3000′ 2000′	0.685	0.014	2.849	0.959	0.196	3.18 5.05	1.055	0.862	2.30 3.21
1400′ 1200′ 1000′	1.928	1.580	1.306	0.579	0.437	3.13 4.92	0.242	0.808	2.24 3.08
Upper three vs. Lower three	6.408*	1.769	38.653**	63.135**	62.858**	3.92 6.84	21.717**	7.828**	2.29 3.17

* Variance ratio exceeds that at 5% level of significance.
** Variance ratio exceeds that at 1% level of significance.

thorax-length and head-width show relatively little change throughout the sampled range. There is not in fact significant heterogeneity for the locality means of these dimensions. Femur-length, wing-length and wing-width on the other hand all show significant heterogeneity and the wing and femur are clearly larger at the upper three than at the lower three elevations.

Tests of heterogeneity between the locality means in the three upper and the three lower levels show lack of heterogeneity within either the upper or lower half of the transect. On the basis of this finding comparisons can properly be made between the upper three and lower three localities. Such comparisons (table 4) indicate that the upper and lower regions differ significantly for four of the five basic measurements, only head-width showing no significant difference between the two regions.

Although the six samples studied show a clear change from the upper to the lower elevations, the over-all form of this change is somewhat obscured by the irregularities in the changes of the five basic characters. In order to clarify and emphasize the over-all change with altitude a compound measurement, Fisher's Discriminant Function, was calculated. This discriminant was so chosen as to discriminate most efficiently between the strains from the upper three and the lower three elevations. It takes the form $D_3 = c_1x + c_2y + c_3z + c_4u + c_5v$, where D_3 is the compound measurement and x, y, z, u and v represent the measurements of the five characters mentioned above, with $c_1 \ldots c_5$ chosen so as to maximize the inter-group variance relative to the intra-group variance. The calculation of such coefficients is discussed by Barnard (1935) and Fisher (1936). The most efficient coefficients for discriminating be-

tween strains from the upper three and lower three locations turned out to be:

thorax-length	$c_1 = -2.0049$
head-width	$c_2 = -1.3549$
femur-length	$c_3 = +4.2632$
wing-width	$c_4 = +1.9866$
wing-length	$c_5 = +1.0000$

Using these coefficients a mean D_3 was calculated for each of the six locations. These values are listed in table 3 and represented graphically (as percentages of unweighted mean D_3 for six locations) in figure 2.

It will be noted that the values of D_3 show a regular gradient through all levels except the last, the trend showing an apparent reversal between 1200 and 1000 feet. The tests of significance for various parts of this series of D_3 values are summarized in the right-hand section of table 4. This table indicates that the apparent reversal in trend of D_3 at the lower levels is non-significant, and that while there is no significant heterogeneity between the localities within the upper three or lower three levels, a comparison of the pooled values for the upper and lower levels shows a highly significant difference. Clearly the major part of the observed change is between the 2000 and 1400 foot levels.

The form of the differences indicated is especially interesting when compared with the differences which exist between northern and southern strains of *D. robusta*. Stalker and Carson (1947) have shown that northern strains tend to have longer wings and narrower heads than those from the south, the correlation between these dimensions and average annual temperature of the source locality being highly significant. No significant correlation of this sort was found in the case of wing-width, and in the case of thorax-length and femur-length the correlations are weak (the correlation coefficients being slightly above that at the 5 percent level of significance). In regard to these last two dimensions there is a tendency for northern strains to have shorter thoraces and longer femora. The comparison between these findings and those reported in this paper is made in table 5.

TABLE 5. *Comparisons of change with altitude and change with latitude (as measured by average annual temperature) for five characters and Discriminant D_2*

Character	Change from North to South	Change from upper to lower elevation
Thorax-length	Increase (weak)	Decrease
Head-width	Increase	No significant change
Femur-length	Decrease (weak)	Decrease
Wing-length	Decrease	Decrease
Wing-width	Non-significant decrease	Decrease
Discriminant D_2	Decrease	Decrease

It will be noted from this table that while strains from upper elevations resemble those from the north in femora and wings, there is lack of agreement in thorax and head. This is especially striking in the case of head-width, which has a very clear correlation with latitude (as measured by average annual temperature).

The agreement in some characters and lack of it in others, make it desirable to calculate some compound measurement, which could indicate over-all resemblance between northern and southern and high and low altitude strains. Stalker and Carson (1947) calculated such a compound, the Discriminant Function D_2, so chosen as to discriminate most efficiently between strains from different climatic zones. This discriminant takes the same form as D_3 above. In this case the most efficient coefficients for discriminating between strains from different climatic zones were:

thorax-length	$c_1 = +0.5030$
head-width	$c_2 = -1.2630$
femur-length	$c_3 = +1.0000$
wing-width	$c_4 = +0.2193$
wing-length	$c_5 = +0.0023$

Using these coefficients a D_2 value was calculated for each of 45 geographical strains. The D_2 values so obtained showed a highly significant negative correlation

with average annual temperature of the source locality.

Thus, since the flies from the north had higher D_2 values than those from the south, a high D_2 is evidently characteristic of a northern type of morphology, and the relative size of the D_2 values should then indicate the "northernness" or "southernness" of the morphology of any group of *D. robusta* adults. If then two groups of flies are compared morphologically, those with a significantly higher D_2 value should be considered as possessing a more northern phenotype than those with the lower D_2 value.

Using the coefficients listed above, a new set of discriminants was calculated for the mountainside population, one mean D_2 being computed for each of the six elevations. These values are listed in the last column of table 3 and shown graphically (as percentages of over-all unweighted mean) in figure 2. Summaries of tests of significance are given in table 4. It will be noted that the D_2 values for the six localities show significant heterogeneity, and that although there is apparently a trend with high D_2 values at higher elevations and low values at low elevations this trend appears to be reversed at the first and last intervals. Tests of the differences between 4000 feet and 3000 feet and between 1200 feet and 1000 feet indicate that this apparent reversal is not significant. Comparison of the pooled D_2 values of 4000 feet, 3000 feet and 2000 feet with those of 1400 feet, 1200 feet and 1000 feet indicates a highly significant difference. Thus there is a tendency for flies from high elevations to have a higher D_2 value; and interpreting the D_2 value as an over-all measurement of the "northernness" or "southernness" of the morphology, the flies from the higher elevations are significantly more "northern" than those from the lower levels.

Discussion

The changes with altitude for the two Discriminants and three most variable single characters appear (in so far as our data are capable of demonstrating them) to occur in two steps, with the greatest changes occurring between the 2000 and 1400 foot levels, and relatively little change of a regular or significant nature occurring above or below this break. This is in marked contrast to the very considerable inversion frequency changes which occur above 2000 and below 1400 feet.

The simplest explanation of this non-parallelism of the cytological and morphological changes would be that the genes responsible for the altitudinal changes in morphology lie almost entirely in the approximately fifty per cent of the chromatin not involved in inversions. However, our study of a Missouri population of *D. robusta* has shown that there are clear morphological characteristics associated with some of the inversions (unpublished data). It seems probable that similar relationships exist in the mountain populations, although the number of measured flies are insufficient to demonstrate them. If we reject as improbable the hypothesis that almost all of the genes controlling the observed morphological differences in the transect lie outside the inversions, two alternate explanations are possible.

1. The genes within the inversions are only partly responsible for the observed morphological changes with altitude. Genes lying outside the inversions are also important and are responsible for the fact that the morphological and cytological changes with altitude are non-parallel.

2. The major portion of the genotype responsible for changes with altitude may lie within the inversions. This could be the case if it were true that the same gene arrangement has different genetic values at the different localities. This assumption would not be out of line with Dobzhansky's findings in *D. pseudoobscura* (unpublished data, cited in 1948 paper). Thus 2L-3, for example, might be somewhat different at 4000 feet and at 1000 feet. But two different types of altitudinal changes must then be explained; the morphological changes based on differences *within* 2L-3 and the cytological changes

based on differences *between* 2L-3 and alternate arrangements. The situation might be visualized as follows: All specimens of 2L-3 contain a certain group of genes which differ from a group found in all specimens of each of the alternate arrangements. It is these genes found in all 2L, 2L-1, 2L-2 or 2L-3 on which selection acts to establish altitudinal differences in inversion frequencies, resulting in the selection of 2L-3 and the discrimination against the alternate arrangements.

But within 2L-3 some genetic heterogeneity may exist which would in turn have selective value, resulting in the selection of one type of 2L-3 at 4000 feet and a somewhat different type at 1000 feet. The type of 2L-3 or the type of any other gene arrangement present in any given population would then determine its morphological characteristics.

We have no evidence that the major portion of the altitudinal change in morphology does depend on genes included in inversions, but suggest the mechanism above in order to show that this is not an impossible situation. Although we have spoken of the possible adaptive nature of the morphological changes it is, of course, understood that these changes may be nonadaptive indications of some more important physiological changes which are themselves adaptive in nature.

Stalker and Carson (1947) suggested that the parallelism in the morphological and cytological geographical clines might indicate that the inversion frequency gradients were responsible for the gradients in the morphology, with the inversions having a high frequency in the north carrying genes which produced a northern phenotype. In view of the apparent dissimilarity between the two types of altitudinal clines, such a rigid relationship between the morphology and gene arrangements seems unlikely.

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Summary

A morphological and cytological study of an altitudinal transect of *Drosophila robusta* Sturtevant was made near Gatlinburg, Tennessee. The transect included six collecting localities extending from 4000 to 1000 feet in altitude and covering a linear distance of eighteen miles.

Eleven out of the fourteen gene arrangements found showed changes in frequency over the area studied. The changes in inversion frequencies with decrease in altitude were not simple recapitulations of changes observed from north to south in geographical studies. Some geographically northern inversions showed no change (2R), or an increase in frequency (3R), with decreasing altitude. In the case of the clearly northern 2L-3 and XL-1 a striking decrease in frequency with decreasing altitude was found. The disagreement between geographical and altitudinal clines in the case of 2R and 3R may be due to the fact that: (a) the environments in the north and at 4000 feet in Tennessee are similar but by no means identical; (b) the same gene arrangement may have different genetic values at different localities.

Of the five morphological characteristics measured in F_2 females, four: thorax-length, femur-length, wing-length and wing-width, showed significant decrease with decreasing altitude. Of these four, femur-length and the two wing dimensions also decrease from north to south. Thorax-length is greatest in the south, and head-width which showed no change with altitude is also greatest in the south.

A compound measurement D_2 (Fisher's Discriminant Function) so chosen as best to discriminate between the upper three and lower three localities indicated that the over-all morphological changes with altitude were greatest between 2000 and 1400 feet, with little change above or below this point. This is in agreement

with the changes in the three most variable single characters, femur-length, wing-length and wing-width. The form of the changes indicated above is in contrast to the changes in inversion frequencies, which were pronounced above 2000 and below 1400 feet. The possible reasons for this discrepancy are discussed.

Using the coefficients associated with the Discriminant D_2, originally chosen so as best to discriminate strains from different climatic zones in the geographical study, a mean D_2 was calculated for each mountain locality. Considering the values of D_2 as measures of "northernness" or "southernness" of the morphology, it was concluded that the populations in the upper levels of the transect are significantly more northern in their morphology than those in the lower levels.

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SPECIATION IN THE FISHES OF THE GENUS *MENIDIA*

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The genus *Menidia,* which includes the common silversides of the Atlantic and Gulf coasts of the United States, presents several aspects of interest for an evolutionary study. Members of this genus have repeatedly entered fresh water from the sea:—two full species, *M. audens* and *M. extensa,* have evolved from such invasions, and there are rather numerous examples of less-marked fresh-water differentiation within *M. beryllina.* Two species, *M. beryllina* and *M. menidia,* occur together along the Atlantic coast from Massachusetts to Florida, thus permitting a comparative analysis of geographic gradients. Furthermore, these same two species hybridize in Florida. Thus, all gradations from incipient speciation to full specific differentiation, with and without hybridization, are found.

According to the most recent treatment (Schultz, 1948), there are only four species in *Menidia;* it is these four that are dealt with here. *M. menidia* is a salt-water form ranging from Nova Scotia to Florida. *M. beryllina* occurs in salt, brackish, and coastwise fresh water from Massachusetts to Vera Cruz, Mexico. *M. audens* is found in fresh water in the lower Mississippi Valley, and *M. extensa* is confined to Lake Waccamaw, a faunistically isolated lake in North Carolina (Hubbs and Raney, 1946). The data to be presented here are focused on *M. beryllina,* for the stock of this species seems to have given rise to *M. audens* and *M. extensa* in one direction and hybridizes with *M. menidia* in another.

The chief characters which have been used in differentiating the forms of the genus are the numbers of anal rays [2] and of vertebrae, the number and degree of development of the scales, the shape of the mouth and snout, the position of the first dorsal fin, the depth of the body, and the location of the posterior extremity of the air bladder.

For a study of geographic variation in *M. beryllina,* various of the characters mentioned above may be used. Those which lend themselves most readily to statistical analysis, however, are the numbers of second dorsal and of anal rays (table 1 and figure 1). Within each of the populations examined (with one exception), these two counts are positively correlated (table 1). However, between populations there is no correlation between these characters (a correlation coefficient calculated between six representative populations gave + 0.04). Apparently some factor associated with geography affects one but not the other of these counts between localities, without disturbing the inherent correlation between these characters at any one locality. If, for marine populations, the average second dorsal counts are plotted against latitude (fig. 2), an increase in dorsal ray count is found

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[2] The methods of making the counts and measurements used in this paper are as follows. The first full-length ray is considered the first ray in the anal and second dorsal, and the last, more or less double, ray is counted as a single ray. The predorsal scale count includes as extremities the first scale behind the dark area of the head and the last normally shaped predorsal scale. The preventral count includes all scales in the midline from the isthmus to the posteriormost scale between the ventral fins. The total scale count is taken along that series which runs just above the pectoral base. The depth of body is measured at the level of the anus. Vertebral counts include the urostyle; the first caudal vertebra is that with the first closed haemal arch.

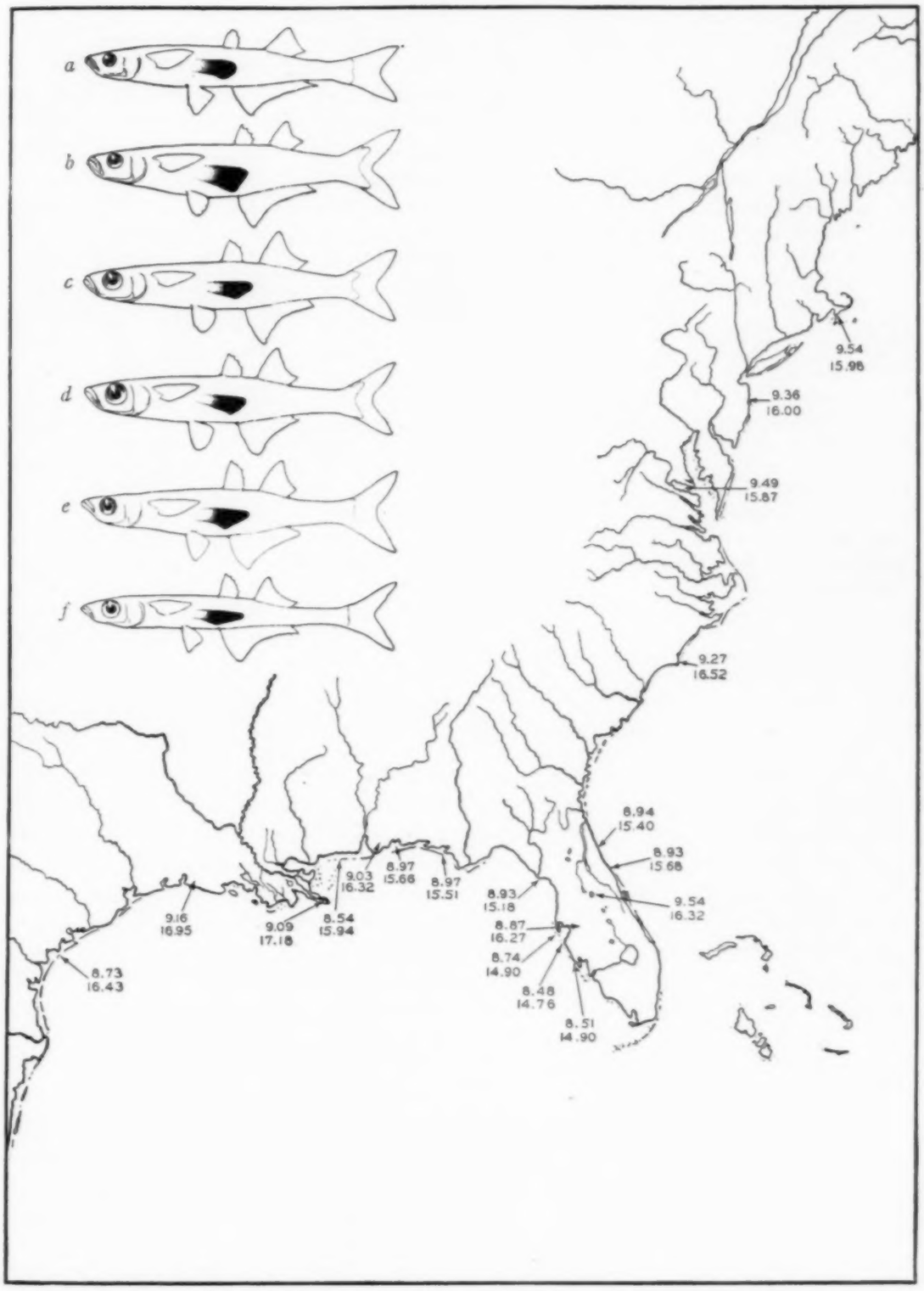

FIG. 1. *Average second dorsal and anal ray counts in various samples of* Menidia beryllina. Dorsal rays are given above, anal rays below for each sample. Insets: a, Massachusetts specimen of *Menidia menidia;* b, Florida specimen of *M. menidia;* c, Massachusetts specimen of *M. beryllina;* d, Florida specimen of *M. beryllina;* e, *M. audens;* f, *M. extensa.* In the insets the position of the posterior extremity of the air bladder is indicated in black. Inset figures a-d redrawn from Kendall (1902).

TABLE 1. *Numbers of second dorsal and anal rays, and correlations between them, in various samples of* Menidia beryllina

Starred samples are those not included in figure 1

Locality	Number of specimens	Second dorsal rays		Anal rays		Coefficient of correlation
		Mean	Standard deviation	Mean	Standard deviation	
Mass.: Barnstable Co.	66	9.54	±.65	15.98	± .89	+.30
N. J.: Ocean Co.	36	9.36	±.67	16.00	± .97	+.55
Md.: Charles Co.	61	9.49	±.69	15.87	± .97	+.66
N. C.: New Hanover Co.	71	9.27	±.58	16.56	±1.02	+.32
Fla.: St. Johns Co.	35	8.94	±.54	15.40	± .59	−.03
Fla.: Volusia Co.	75	8.93	±.61	15.68	± .85	+.61
Fla.: Lake Co.	37	9.54	±.60	16.32	± .64	+.39
Fla.: Charlotte Co.	70	8.51	±.65	14.90	±1.00	+.50
Fla.: Manatee Co.	50	8.48	±.57	14.76	± .73	+.57
Fla.: Pinellas Co.	113	8.74	±.54	14.90	± .91	+.50
Fla.: Hillsborough Co.	55	8.87	±.66	16.27	± .88	+.37
Fla.: Levy Co.	28	8.93	±.65	15.18	±1.04	+.71
Fla.: Bay Co.	66	8.97	±.58	15.51	± .89	+.38
Fla.: Santa Rosa Co.	67	8.97	±.46	15.66	± .80	+.66
Ala.: Baldwin Co.	31	9.03	±.60	16.32	± .96	+.38
Miss.: Jackson Co.	52	8.54	±.77	15.94	±1.01	+.48
Miss.: Jackson Co.*	65	8.80	±.56	16.15	±1.10	+.33
Miss.: Jackson Co.*	50	9.00	±.66	16.60	± .98	+.52
La.: Orleans Parish*	80	9.09	±.57	17.11	±1.20	+.40
La.: Plaquemines Parish	54	9.09	±.62	17.18	± .94	+.38
La.: Cameron Parish	44	9.16	±.56	16.95	±1.00	+.38
Texas: Aransas Co.	60	8.73	±.66	16.43	± .96	+.37

from south to north. However, the number of anal rays shows at best an erratic increase with latitude. For example, the average anal counts in many Gulf Coast samples (table 1 and fig. 1) is higher than that from Massachusetts. It is apparently this geographic fluctuation in anal count, as opposed to a rather level gradient in dorsal count, which causes the lack of correlation between these two characters between populations.

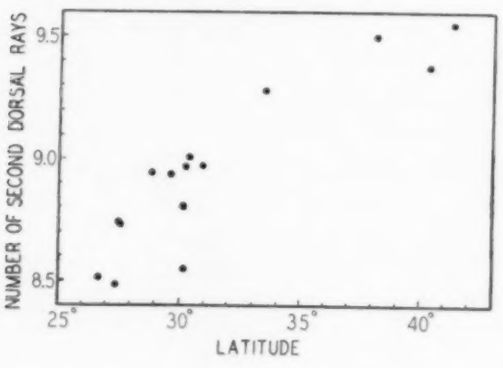

FIG. 2. *Correlation between number of second dorsal rays and latitude in marine samples of* Menidia beryllina.

In neither the dorsal nor the anal counts do the marine populations of *M. beryllina* show a continuous gradient from Texas to Massachusetts (table 1 and fig. 1). Rather, fish from both coasts of the Florida peninsula are set off by their minimal fin counts from the populations both to the northeast and to the west.

If only the marine populations of *M. beryllina* are considered, it might be possible on the basis of fin counts to divide the species into two or more, relatively homogeneous races. However, the situation is greatly complicated by the populations of this species which occur in fresh water. Such populations have been taken on Long Island, in the Potomac River, in North Carolina (Kendall, 1902, pp. 259 and 260), and from various localities in Florida and near the Gulf Coast. The fresh-water populations seem to differ from the salt-water fish in having a

greater number of soft fin rays and scales, and, with some exceptions, in having a more elongate body. The relationship of these characters to decreasing salinity may be traced in series of adjacent populations (table 2). The two Florida series shown in this table consist of two populations each, one from fresh water and one marine. But the same gradient seems to apply in the three more or less marine populations from near Biloxi. Also, from the point of view of geographic proximity those samples beginning with that from the outer shore of Horn Island to the one

TABLE 2. *Change in morphological characters from salt to fresh water in* Menidia beryllina *and related fresh-water species*

Means are given above, and number of specimens and standard error of the mean below in parentheses. Data for the starred item from Hubbs and Raney (1946).

Locality	Salinity	Anal rays	Second dorsal rays	Predorsal scales	Depth of body in per cent of standard length
M. beryllina					
East-Central Florida					
Volusia Co.	Salt?	15.68 (75, ±.10)	8.93 (75, ±.07)	14.2 (10, ±.25)	20.8 (10, ±.19)
Lake Eustis, Lake Co.	Fresh	16.32 (37, ±.10)	9.54 (37, ±.10)	15.5 (10, ±.37)	17.3 (10, ±.27)
West Coast of Florida					
Pinellas Co.	Salt	14.90 (113, ±.09)	8.74 (113, ±.04)	14.4 (10, ±.30)	20.2 (10, ±.29)
Hillsborough Co.	Fresh?	16.27 (55, ±.12)	8.87 (55, ±.09)	15.4 (10, ±.23)	18.0 (10, ±.19)
Biloxi, Mississippi region					
Horn Island, seaward side	Salt	15.94 (52, ±.14)	8.54 (52, ±.11)	15.7 (20, ±.18)	18.1 (10, ±.23)
Horn Island, landward side	Salt	16.15 (65, ±.14)	8.80 (65, ±.17)	15.0 (20, ±.16)	17.8 (10, ±.16)
Biloxi Bay	Brackish?	16.60 (50, ±.14)	9.00 (50, ±.09)	15.8 (20, ±.12)	18.5 (10, ±.34)
Lower Mississippi valley					
Lake Pontchartrain	Fresh?	17.11 (80, ±.14)	9.09 (80, ±.06)	15.8 (20, ±.20)	17.8 (10, ±.24)
Mississippi delta	Fresh?	17.18 (54, ±.08)	9.09 (54, ±.04)	15.7 (20, ±.16)	18.0 (10, ±.23)
M. audens					
Ark., Chicot Co.	Fresh	18.24 (53, ±.11)	9.37 (53, ±.08)	19.4 (20, ±.32)	16.0 (10, ±.25)
Tenn., Reelfoot Lake	Fresh	17.72 (54, ±.14)	9.24 (54, ±.09)	21.8 (20, ±.36)	16.2 (10, ±.20)
M. extensa					
North Carolina					
Lake Waccamaw*	Fresh	19.05 (43, —)	9.4 (43, —)	22.0 (18, —)	13 (19, —)

from the Mississippi delta might be considered as one continuous series. Kendall (1902) found the same character gradient in the Potomac River. The conclusion that changes in these four characters are correlated with salinity seems inescapable.

Two fresh-water species of *Menidia* have been described, both of which seem distinct from one another and from *M. beryllina* (tables 2 and 3). *M. audens* is now distributed over a moderately large area of the lower Mississippi valley; it appears to be monophyletic. Structurally, though probably not phylogenetically, it is transitional between *M. beryllina* and *M. extensa* (Hubbs and Raney, 1946). *M. extensa* is the most elongate species in the genus, with an increased number of fin rays, scales, and vertebrae. In all of these characters, except perhaps vertebrae, both *M. audens* and *M. extensa* appear to represent continuations of the salt-to-fresh-water gradient indicated for *M. beryllina*.

In other fishes that have been studied there is usually an increase in meristic counts, not with decrease, but rather with increase in salinity. As a matter of fact, the typically marine species *M. menidia* shows such an increase in counts over *M. beryllina*, which is essentially a brackish-salt-water form (table 3). However, the cause of these high counts in *M. menidia* lies, I believe, in geography, as I shall point out below. However, because of the relatively large number of meristic elements in *M. menidia* the possibility exists that *M. audens* and *M. extensa* are derivatives of this species rather than of *M. beryllina*. This seems unlikely for several reasons. Although *M. menidia* is found on the Carolina coast near *M. extensa*, it does not occur off the mouth of the Mississippi through which *M. audens* must have gone. *M. menidia* rarely occurs in fresh or even in brackish water. A chain of morphologic forms has been shown to link *M. extensa* with *M. beryllina*. In *M. menidia* the air bladder does not reach much beyond the anal origin whereas in *M. beryllina*, *M. audens*, and *M. extensa* respectively it extends backward beyond that point in increasing amounts (fig. 1, insets, and table 3[3]). Thus in the development of the air bladder *M. beryllina* is a logical intermediate between *M. extensa* and *M. menidia*.

The question remains then as to the

[3] The increased length of the air bladder is reflected in the higher number of abdominal vertebrae (or vice versa) shown for *M. audens* and *M. extensa* in table 3.

TABLE 3. *Comparison of morphological characters in the four species of* Menidia

Data for the starred items from Hubbs and Raney (1946). Means are given above, and number of specimens and range below in parentheses.

Species and locality	Abdominal vertebrae	Caudal vertebrae	Total vertebrae	Number of anal rays with base under air bladder	Scales	Anal rays	Snout-dorsal distance in per cent of length
Menidia menidia Massachusetts	19.2 (8; 18–20)	24.8 (8; 24–26)	44.0 (8; 43–45)	0.5 (4; 0–1)	45.8 (6; 44–48)	23.3 (10; 21–25)	51.7 (10; 50.2–53.3)
Florida	16.7 (10; 15–19)	22.7 (10; 22–24)	39.4 (10; 37–42)	0.8 (4; 0–2)	39.9 (9; 37–43)	22.2 (10; 21–24)	57.3 (10; 54.0–59.7)
M. beryllina Massachusetts	18.4 (15; 17–19)	20.0 (15; 19–21)	38.4 (15; 37–39)	3.2 (4; 2–4)	39.2 (10; 37–41)	15.98 (66; 14–19)	51.6 (10; 48.4–53.3)
Florida	18.1 (10; 17–19)	19.7 (10; 19–21)	37.8 (10; 37–39)	3.0 (4; 3–3)	39.9 (9; 37–43)	15.40 (35; 14–16)	53.3 (10; 52.3–54.8)
M. audens Arkansas	19.7 (10; 18–21)	19.6 (10; 19–21)	39.3 (10; 38–42)	6.0 (10; 4–8)	40.9* (20; 39–44)	18.15* (20; 16–20)	50.2 (10; 48.1–53.2)
M. extensa North Carolina	22.5 (2; 22–23)	20.5 (2; 20–21)	43.4* (13; 42–45)	7.5 (2; 7–8)	46.4* (25; 44–50)	19.05* (43; 16–21)	49.8 (10; 48.4–50.7)

relationship between *M. beryllina* and *M. menidia*. The latter species, as stated, shows an increase in meristic counts over *M. beryllina* (table 3). In the area between Massachusetts and Florida where the two species occur together, the direction of the morphological gradients is the same, but the degree to which these gradients are developed is very different. *M. beryllina* shows very little south-north increase, whereas *M. menidia* has developed into two subspecies well differentiated in the number of meristic elements (Kendall, 1902). Of these two subspecies, the southern in most respects resembles *M. beryllina* far more than the northern (table 3).

Finally as mentioned in the introduction, hybrids between *M. menidia* and *M. beryllina* have been found in northern Florida (Hubbs and Raney, 1946, p. 23). In the Michigan collections, hybrids between these two species were identified by Hubbs from two salt- or nearly salt-water localities in northeast Florida: Matanzas River, about 1½ miles south of Matanzas Inlet (called Matanzas Inlet population in table 4), St. Johns County; and Mosquito Lagoon, between Daytona Beach and Mosquito Inlet. (Both parent species were taken with the hybrids.) In order to verify the hybrid nature of these fishes, I have chosen four more or less independent characters which permit separation of the parent species in the area concerned. Means, their standard errors, and sample standard deviations for these characters are given in table 4. The degree of intermediacy of the hybrids between the means of the parent populations is shown in fig. 3.

One possibility in connection with these two populations is that such hybrids are fertile and, by backcrossing with one or both parents, contribute to the resemblance between the parent species in southern waters. The best check available on this point is a sample of pure *M. menidia* from the Matanzas River. This collection shows no significant differences from the Matanzas River Inlet population in which hybrids occur (table 4), indicating the conclusion that backcrossing has at least not effectively modified the *M. menidia* population in the Matanzas River Inlet.

On the basis of the foregoing data, certain conjectures concerning the processes of speciation in the genus *Menidia* may be permitted. In the first place, it seems fairly clear that *M. audens* has developed through invasion by *M. beryllina* stock of the Mississippi, and by subsequent isolation and differentiation in the lower Mis-

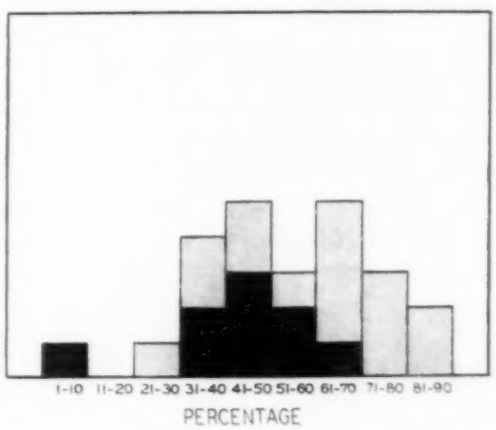

FIG. 3. *Degree of intermediacy between hybrids and their parent species,* Menidia beryllina *and* M. menidia. Percentage intermediacy calculated according to the formula

$$\frac{100(\text{hybrid value} - \text{mean of } M.\ beryllina)}{\text{mean of } M.\ menidia - \text{mean of } M.\ beryllina}$$

for each of the four characters shown in table 4 and the characters averaged. According to this method of calculation true *M. beryllina* would show a peak around 0 and true *M. menidia* a peak around 100. The nine Matanzas Inlet hybrids are shown in black and the fifteen Mosquito Lagoon hybrids in the stippled area.

sissippi valley. *M. extensa* seems to have become isolated from the Atlantic coastal stock of *M. beryllina* when Lake Waccamaw became separated from the sea in late Pleistocene time (Hubbs and Raney, 1946).

The present relationship between *M. beryllina* and *M. menidia* appears to have had a more complex history. Both these species increase in the number of meristic counts to the northward; also, *M. menidia* has higher meristic counts than *M. beryl-*

TABLE 4. *Comparison of morphological characters between* Menidia beryllina, M. menidia, *and hybrids between the two*

"P." equals the probability that the samples of *M. menidia* from Matanzas River and that from Matanzas Inlet were taken from the same population. Means are given above, and number of specimens, standard error of the mean, and range below in parentheses.

Character	*Menidia beryllina*	Difference between means of hybrid and of *M. beryllina*	Hybrid	Difference between means of hybrid and of *M. menidia*	*M. menidia*	Population of pure *M. menidia* from the Matanzas River	P.
No. of specimens							
Mosquito Lagoon	78		15		8		
Matanzas Inlet	34		9		99		
Anal rays							
Mosquito Lagoon	15.68 (75, ±.04) (13–19)	4.02	19.70 (15, ±.24) (18–22)	3.30	23.00 (8, ±.42) (22–25)		
Matanzas Inlet	15.40 (35, ±.03) (14–16)	3.16	18.56 (9, ±.36) (17–20)	3.44	22.00 (10, ±.60) (20–24)	22.20 (10, ±.42) (21–24)	.76
Predorsal scales							
Mosquito Lagoon	14.25 (8, ±.25) (13–15)	2.95	17.20 (15, ±.19) (16–18)	1.18	18.38 (8, ±.35) (17–20)		
Matanzas Inlet	14.30 (10, ±.23) (13–15)	1.48	15.78 (9, ±.27) (14–17)	1.82	17.60 (10, ±.24) (17–19)	17.30 (10, ±.37) (16–19)	.60
Preventral Scales							
Mosquito Lagoon	14.25 (8, ±.30) (13–15)	1.48	15.73 (15, ±.24) (13–17)	.77	16.50 (8, ±.50) (15–19)		
Matanzas Inlet	12.80 (10, ±.33) (11–14)	1.31	14.11 (9, ±.35) (13–16)	2.09	16.20 (10, ±.44) (14–18)	16.20 (10, ±.42) (14–19)	1.00
Snout-dorsal (in per cent of length)							
Mosquito Lagoon	51.89 (8, ±.44) (49.7–53.5)	3.49	55.38 (15, ±.26) (53.2–57.1)	2.61	57.99 (8, ±.34) (56.8–59.7)		
Matanzas Inlet	53.27 (10, ±.24) (52.3–54.8)	1.75	55.02 (9, ±.47) (52.2–57.3)	2.24	57.26 (10, ±.58) (54.0–59.7)	56.60 (10, ±.25) (55.5–57.6)	.29

lina. Therefore, it seems that an original *beryllina-menidia* stock may have split into a northern form which is now *M. menidia* and a southern form, now *M. beryllina.* This suggestion is strengthened by the fact that now *M. beryllina* ranges farther to the south (to which it has presumably become better adapted) than *M. menidia,* whereas the latter extends farther to the north.

It may be further speculated that this split in the *beryllina-menidia* stock was

caused by the rise of the Florida peninsula from the sea, leaving the ancestors of *M. beryllina* in the Gulf of Mexico and those of *M. menidia* on the Atlantic Coast. Under this hypothesis *M. beryllina* would have since spread up the Atlantic Coast. That *M. menidia* is the older form of the two along this coast is suggested by the fact that it has formed two well-differentiated subspecies there, whereas *M. beryllina* has not. However, if *M. beryllina* is postulated as the ancestor of *M. extensa*, *M. beryllina* must have been along the Carolina coast in the Pleistocene.

If the two species have lived together on the Atlantic Coast since the Pleistocene, the question arises, why do they now hybridize in Florida? This question does not reflect adversely upon the hypothesis set forth, since it would have come up in connection with any hypothesis whatever. Perhaps the best answer is that *M. menidia* is now in the process of extending its range southward, and that its southern outposts undertake spawning under conditions which they do not encounter in their normal range. These conditions in Florida might include such factors as overlap in spawning season or habitat with *M. beryllina*, the absence of sufficient numbers of *M. menidia* to undertake spawning alone, etc.

I wish to thank R. M. Bailey and E. T. Hooper of the Museum of Zoology, University of Michigan, for reading this paper and for suggestions concerning the hypothetical treatment of the processes of speciation in the genus. All specimens reported on in this paper are in the University of Michigan collections.

Summary

The phylogeny of the genus *Menidia* was approached through a study of morphological characters, ecology, and geographical distribution of the four species now attributed to the genus. The two fresh-water species, *audens* (Lower Mississippi Valley) and *extensa* (Lake Waccamaw, North Carolina), appear to be recent (Pleistocene or later) derivatives of the stock of *beryllina*, a species now abundant in coastal salt and fresh water along the Atlantic Coast from Vera Cruz, Mexico to Massachusetts. The two coastal species, *beryllina* and *menidia*, seem to have evolved from a single ancestral form through geographical isolation and differentiation in a northern group of populations, now represented by *menidia*, and a Gulf of Mexico population, now represented by *beryllina*. There is some hybridization between the species *menidia* and *beryllina* in northern Florida, and a preliminary analysis indicates that this hybridization has not altered the phenotypic characters of populations of the parent species *menidia* from the same area.

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GLACIATION, AN ISOLATING FACTOR IN SPECIATION

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Geographical isolation seems to be a necessity for a species to break up into daughter species. The evidence for this is so great that apparent exceptions are of particular interest, as providing opportunities to test the generalization. On continental areas when species with widespread, continuous ranges break up into subspecies the usual pattern is for a gradual change in characters, from one to the other, this area of change being wider or narrower, depending on the abruptness of ecological change in the habitat. In northern continental North America most forms agree with this, but there are a number of non-conforming examples. These are cases where two representative forms with a continuous range have evolved beyond the point where they behave as subspecies to each other, but have not yet attained all the attributes of species in respect to each other. There are two alternative explanations. Either they have evolved in situ without the aid of geographical isolation, or some factor in their history has provided an isolation since removed. It is such cases, from the northern part of North America, which I discuss below, with the suggested explanation that former isolation provided by the ice age is sufficient to account for present conditions.

Much of northern North America has been occupied, or re-occupied, only recently by its present biota. Presumably before the ice age there was a northern transcontinental belt occupied by plants and animals. But when glaciers came to cover most of the northern part of the continent, the plants and animals living there were reduced to existing in refugia south of the ice, and in ice-free refugia within the glaciated area. Later with the melting and retreat of the ice the biota again spread to occupy the northern part of the continent.

One effect of this glaciation was to provide isolation for the fragments of populations of the various species, in which they could evolve independently, with resulting complexities when later the descendants of these isolated populations met, after the melting of the ice. This aspect of speciation has received some attention particularly by botanists (see Raup, 1946, and Hulten, 1937) and has been considered in working out the taxonomy of certain birds, notably the relation of bronzed and purple grackles *Quiscalus quiscula aeneus, quiscula* and *stonei* (Chapman, 1940) and the yellow shafted and the red shafted flickers (*Colaptes auratus* and *C. cafer*) (Mayr, 1942, p. 265). In the European area a similar set of phenomena has received considerable attention (see Mayr, 1942, pp. 263–5) but in North America this subject merits additional study. In a review of the history of the North American bird fauna Mayr (1946) does not discuss the effect of glaciation.

The effects of this glaciation are particularly apparent where pairs of "semispecies" were formed. These are the cases in which two forms, or groups of forms, meet along a narrower or wider belt, and their relationships to each other are neither those of species, nor those of subspecies, but combine some characteristics of each. They seem to be, and in all probability are, at a stage of evolution between that of species and of subspecies. It has been suggested that these are "species in the making," and present day barriers, such as the Rocky Mountains, are sufficient to account for this process (Mayr, 1940, p. 260). However from personal examination of much of this

FIG. 1. Maximum extent of solid ice sheets according to Hulten, 1937; additional local glaciation also occurred. Flint (see fig. 2) believes that glaciation was more extensive than this.

country, no present day barriers are apparent. If we accept these "semi-species" as the product of conditions as they exist today, we would have to dismiss physical isolation as an important factor in their speciation. As I shall show below, this speciation correlates with the isolation of an earlier glacial period, and the present zone of contact is a secondary one.

The botanists have postulated refugia; one or more southeast of the ice; two or more southwest of the ice in the Rocky Mountains area; and one or more in the Yukon-Bering Sea area (Raup), which correlate with types of bird distribution. In addition certain groups of "semi-species" indicate there might have been refugia in the Arctic Islands. These last need not have been permanent in location. They could have been slowly moving, and transient for any one locality.

In the following I discuss examples which seem to correlate with the refugia outlined above (figs. 3–5).

The suggestion of refugia in the Arctic islands comes from the Herring-Iceland Gull (*Larus argentatus-L. leucopterus*) complex. *Larus leucopterus* breeds in Greenland; *kumlieni* on Baffin Island; *thayeri* on the other Arctic Islands and the adjacent arctic coast. All behave as subspecies to each other. *L. a. smithsonianus*, a more southern form which seems to be subspecifically related to *thayeri*, however, also breeds on Baffin Island where it meets *kumlieni* as a species. Here we get a circle of subspecies, with the end products behaving as species, this last certainly being a secondary condition (Rand, 1942).

A related case is provided by the Canada goose complex (*Branta canadensis*). There are small northern forms which nest

locally on islands and the edge of the arctic coast, while there is a group of larger, more widespread and southern ones. A small overlap in breeding range is recorded (Aldrich, 1946). There is a further complication in the relationships of birds from the northwest area (Alaska and British Columbia) which are dark breasted and by some are considered another, closely related species. The relationships are still incompletely understood.

In the case of both the gulls and the geese a former separation and later meeting after a removal of a barrier seems indicated. For the northern forms a period of isolation of the breeding range by ice masses from the southern forms, and a later meeting with disappearance of the ice might explain the present situation in part. With the geese the additional complication of the dark-breasted, northwestern forms might be correlated with the Yukon-Bering Sea refugia.

A different pattern of speciation correlated with glaciation in the far north is given by the American and the Black Brant (*Branta bernicla* and *B. nigricans*). In America the former breeds in the Eastern Arctic; the latter in the Western Arctic. Apparently they meet somewhere in the Central Arctic but some biological discontinuity seems indicated from the scarcity of intermediates. A similar situation prevails with the Pacific Eider (*Somateria v-nigra*) of the Western Arctic and the Atlantic Eider (*S. mollissima*) of the Eastern Arctic. Certainly a former separation and a later meeting seems indicated. This would correlate with the glacial period, with eastern and western maritime populations separated by the

FIG. 2. Principal areas in the Nearctic that were covered by glaciers at the maximum of the last (Wisconsin) glacial age (Flint, 1947).

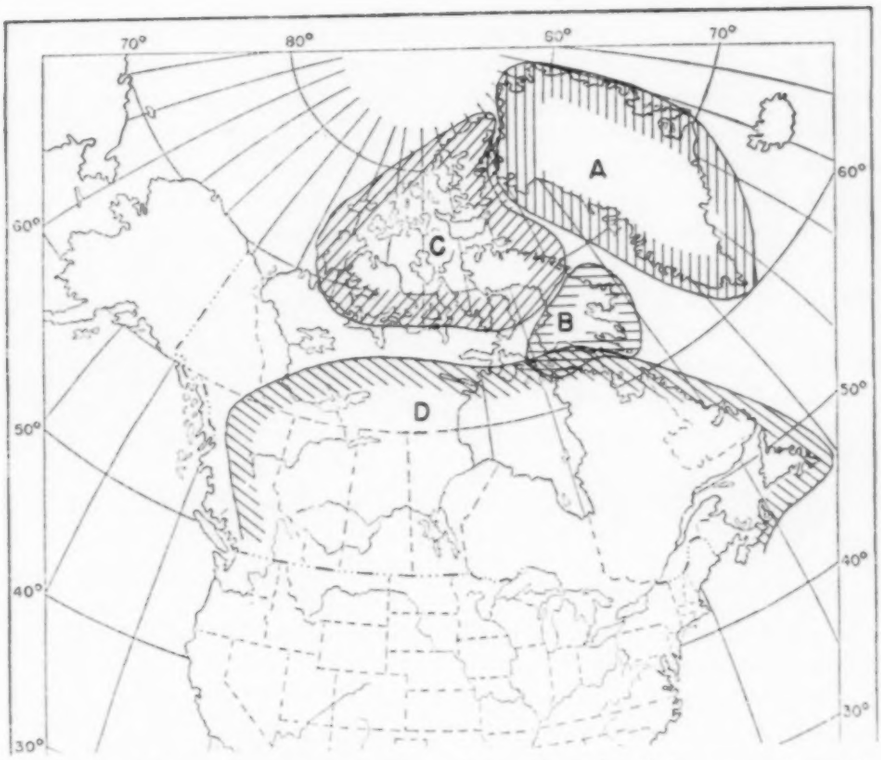

FIG. 3. Outline of breeding ranges of certain gulls of the genus *Larus* in the Nearctic. A. *leucopterus*, B. *kumlieni*, C. *thayeri*, D. *smithsonianus* (after Rand, 1942).

breadth of the ice, and the subsequent meeting following the disappearance of the ice.

The effect of the Yukon-Bering Sea refugia and a southeastern one seems indicated by the Yellow-billed Loon (*Gavia adamsii*) and the Black-billed Loon (*Gavia immer*). The former breeds on the barren grounds from Alaska to Eastern Keewatin; the latter on the lakes of the transcontinental coniferous belt, and of the barren ground of Baffin Island. Very similar morphologically, they appear not to interbreed, but their close relationship is indicated by their ranges being mutually exclusive. A habitat difference, determining their line of meeting, is apparent west of Hudson Bay, but east of Hudson Bay the forest species perhaps reached the barrens of Baffin Island before *adamsii* did and finding it vacant occupied it. This prevented *adamsii* from entering this area. Speed of dispersal as well as point of origin and habitat preference has played a part in present distribution (fig. 4).

A similar situation obtains with the two brown-backed chickadees, *Parus hudsonicus*, the transcontinental boreal forest species, and *P. cinctus*, in America occurring only in the extreme northwestern boreal forest (Alaska to Northern Mackenzie). They are very similar in appearance but their ranges are mutually exclusive (Murie, 1928). Their evolution seems to have reached the same stage as that of the loons discussed above, and presumably against the same background.

A pattern of distribution and relationships correlating with a refugium south of the ice in the east and another south of the ice in the west is given by the Spruce Grouse (*Canachites canadensis*), with a continent-wide distribution from Nova Scotia to Alaska and northern British Columbia, and Franklin's Grouse (*C. franklini*) in the western mountains north to central western Alberta and central British Columbia. The two forms meet in western Alberta, and in the mountains of British Columbia. Morphologically the

two forms are very close, and while intergradation (or hybridization) does occur, it seems not to be common, and intermediates occur over a very narrow zone.

A similar case is provided by the Audubon and the Myrtle Warbler, *Dendroica auduboni* and *D. coronata*. The juncos in the north, the Slate-colored Junco, *Junco hyemalis*, and the Oregon Junco, *oreganus*, present a somewhat similar picture, but the area of meeting is somewhat farther north, northern British Columbia and southern Yukon, as well as in western Alberta, and the zone of intergradation is great enough for the intermediates to receive a name: *J. h. cismontanus* (Miller, 1941).

An effect of two refugia south of the ice in the Rocky Mountains region, as well as one in the southeast, seems indicated in the Canada Jay, *Perisoreus canadensis*, of the coniferous forests. One type of plumage occurs from Nova Scotia to Alaska, *"canadensis"*; another occurs in the mountains from southern British Columbia southward, *"capitalis"*; and a third in the coastal areas from British Columbia southward, *"obscurus."* Though morphologically easily recognizable, they are close; and areas with intermediate populations occur in some places, though in others they are very narrow or lacking.

A somewhat similar picture, though with minor complexities, is presented by the three sapsuckers, the Yellow-bellied Sapsucker (*Sphyrapicus varius*), the Red-naped Sapsucker (*S. v. nuchalis*) and the Red-breasted Sapsucker (*S. v. ruber* and related forms).

There is another example in the White-crowned Sparrow group, *Zonotrichia leucophrys*, which seems to indicate the effects of four populations isolated: one in the southeast; one in Yukon-Bering Sea area; one in the Rocky Mountains area, and one in the Pacific area during glacial periods and since spreading and meeting. The White-crowned Sparrow (*Z. l. leucophrys*) ranges from Gaspé to northern Manitoba; Gambel's Sparrow (*Z. l. gam-*

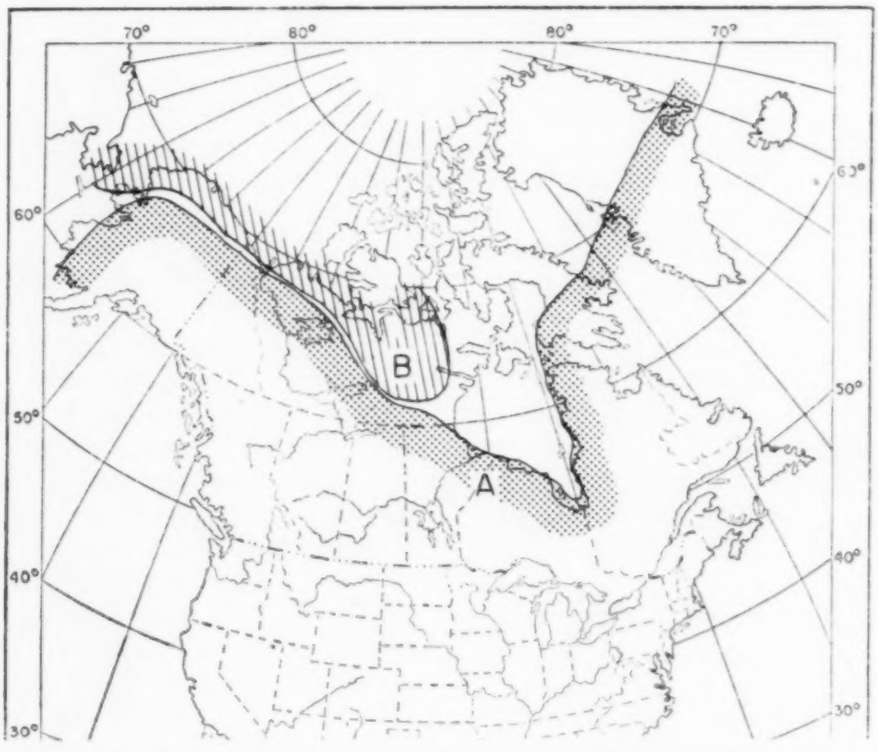

FIG. 4. Northern limit of breeding range of Black-billed Loon, *Gavia immer* (A), and the southern and eastern limits of the breeding range of the Yellow-billed Loon, *Gavia adamsii* (B), in the Nearctic.

FIG. 5. Breeding ranges of the various races of white-crowned sparrows, *Zonotrichia leucophrys*. 1. *leucophrys*, 2. *gambelii*, 3. *nuttalli* and *pugetensis*, 4. *oriantha* (modified from Swarth, 1926).

belii) from northern Manitoba to Alaska and central British Columbia; the Mountain White-crowned Sparrow (*Z. l. oriantha*) from the mountains of southern British Columbia and Alberta southward; and the Puget Sound Sparrow (*Z. l. pugetensis* and *nuttalli*) from coastal southern British Columbia southward. Biological discontinuity is partial between certain populations. These distributions correlate surprisingly well with the distribution of the four closely related spruce trees: white spruce, Alberta spruce, Engelmann spruce, and Sitka spruce, as worked out by Halliday and Brown (1943), who correlate this distribution with the four refugia outlined above.

As a possible alternative there is the question as to whether or not a habitat difference rather than geographical isolation could have been a factor in the evolution of these pairs of northern forms. With the forest and forest edge birds such as chickadees (*Parus*), grouse (*Canachites*), warblers (*Dendroica*), juncos (*Junco*), Canada jays (*Perisoreus*), sapsuckers (*Sphyrapicus*), and white-crowned sparrows (*Zonotrichia*), this definitely does not seem to be the case. The western forests may have conspicuous species of plants different from those of the east, but the gross appearance of the continuing habitat occupied by these birds in each is much the same. With the birds nesting on the barrens along the arctic coast, the brant (*Branta bernicla* and *B. nigricans*) and the eiders (*Somateria*), the same is true; there seems no conspicuous differences in habitats between the east and west.

Habitat differences are correlated in part with speciation in the remaining three complexes. In the loons (*Gavia*) west of Hudson Bay such a correlation appears, but it breaks down east of Hudson Bay; in the gull complex (*Larus*) the northern forms *thayeri-kumlieni-leucopterus* seem more maritime than does the more southern *smithsonianus*. It might be argued that *smithsonianus* had been isolated in fresh-water breeding sites and had only recently spread north to intrude into the area occupied by *kumlieni*, but this does not accord with the habits of the bird farther south, where it nests on salt as well as on fresh water. The case of the Canada geese (*Branta canadensis* and relatives) seems to involve coastal and inland forms, but the habitat relations as well as the taxonomic relationships still remain to be worked out and it seems advisable to correlate them with the explanation that fits better the bulk of the material.

The ecological approach seems unsatisfactory and the temporary geographical isolation founded by glaciation seems the most satisfactory.

Discussion

The above described cases are types of distribution and relationships of "semi-species" in the northern North American bird fauna. Present geographical isolation and habitat differences are insufficient to account for their development. But the present day situation in the avifauna is consistent with a former set of barriers, since removed. And just such a temporary barrier, the ice of the Pleistocene, has been postulated by geologists and extensively utilized by botanists, in solving such problems. It seems to be applicable to the bird fauna also. It is probable that some bird populations were isolated in refugia south of the ice in the east; in the west; and also in the Yukon-Bering Sea area; and perhaps in the Arctic Islands.

We have had in effect a natural experiment in speciation. After a period of isolation the barriers were removed and the populations that had been separated allowed to come together. We can now study the results.

The semi-species which were one of the results did not all evolve uniformly to the same level, in all their characters. In the loons and the chickadees the biological discontinuity appears complete, but their ecological requirements are so similar they cannot invade each other's range. That this is not solely a habitat difference is shown by the loons.

In others, such as in the grouse and in the warblers, there appears to be a partial biological discontinuity. Locally at least there seems little or no discontinuity in the jays and in the juncos.

Though I have followed current practice in calling these related forms "semi-species," and they are at an evolutionary level intermediate between that of species and subspecies, they are not necessarily "species in the making." The two loons and the two chickadees may come to invade each other's territory and behave like ordinary sympatric species; the warblers and grouse may increase their biological discontinuity and evolve to species level with the start they now have. The juncos seem to have established themselves at a subspecies level as have the jays. Some may be species in the making, but others seem to be merging after a period of separation.

The above given examples, of course, do not exhaust the effects of glaciation. Even within the boreal part of the continent it is probable that certain subspecific and specific limits have been affected by the glacial period. It is possible that, in addition to the physical isolation of the ice, eastern and western refugia for boreal forms south of the ice have been separated in part by the treeless steppe extending south of the ice in the central part of the continent. Farther south, glaciation plus geographical isolation caused by ecological factors appears to have been a factor in speciation, including the production of some semi-species. However the present paper is restricted in scope to demonstra-

tion of how certain boreal semi-species could have come into existence.

Summary

A number of northern North American birds have a more or less continuous range in which some geographical representatives are further evolved than the subspecies stage, but have not reached the species stage. If these evolved under present conditions they would appear to be cases of speciation without geographical isolation. However, a factor in their history seems to be the glacial period which provided temporary geographical barriers so that fragments of the species had isolation in which to develop. With the retreat of the glaciers these populations met again, and now show various degrees of relationships between that of subspecies and species. Some may be "species in the making," but others may be merging.

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SOME PROBLEMS AND PATTERNS OF EVOLUTION EXEMPLIFIED BY FOSSIL INVERTEBRATES

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INTRODUCTION

A systematic biologist or a paleontologist inevitably comes to entertain some views about probable modes and patterns of organic evolution. The patterns become delineated according to the group or groups of organisms with which one is familiar, his knowledge of their past record and their present development and distribution, his degree of understanding of the facts and principles of allied biological disciplines, and his acquired prejudices. The modes a systematist conceives to have operated in evolution, however dimly held or naïvely attained his views may be, affect the arrangements he makes and the interpretations that he draws from these arrangements.

It is of fundamental importance that this be recognized and taken into account. It is, moreover, desirable that workers in the several fields of biological science periodically review the principles that they have come to accept and lines of thought that derive from or lead to acceptance of these principles. In the ensuing pages I shall attempt to give expression to some views about relationships between invertebrate paleontology and evolutionary theory, with special reference to modes and patterns of invertebrate evolution.

The paleontologist, of course, is concerned not only with the highly important task of compiling the roster of extinct organisms. He is also interested in the conditions under which the bygone organisms of the earth lived, in their relationships to one another, in how they came to be different from or like one another, and in the reasons why the succession of known forms developed in the order he sees and not according to some other arrangement. Including the living and the dead, there are perhaps a million described species of animals without backbones and another million or so—perhaps several million—yet to be described. These are included in some tens of thousands of genera and thousands of families that are already known and described, and all are grouped in at least a couple of dozen *bona-fide* Phyla.[1] It is fundamental and obvious to inquire how the record of fossil and living animals may be interpreted to indicate relationships and suggest the course of events, and it is about such essentially phylogenetic problems that most paleontological thought on evolution turns.

Of the general subjects that I consider of special interest as regards interpretation of the invertebrate record, three will be discussed in the present paper. These are (1) *homeomorphy*, due either to parallelism or to convergence; (2) *paedomorphosis;* and (3) *eruptive evolution.*

This discussion is presented in all humility, without thought that it is definitive or that more than a very small part of what it contains is truly original. It will fulfill its intention if it brings a few ideas to focus and elicits further discussion of the principles and facts involved. It is to be hoped that systematic tracing of lineages through time with these concepts in mind, and with paleoecologic controls,

[1] The arch reactionary says 9, the most extreme split that I can find reasonable basis for gives 35. It is to be noted that by the word *Phylum* I mean the largest formally recognized systematic category below an infra-kingdom, in distinction to some current usage of the term to mean any phyletic line. The initial capital P is used advisedly to emphasize this distinction.

may eventually furnish the statistical basis for more objective causal interpretations.

Acknowledgments

Clearly one's thoughts on so broad a subject as evolution will be influenced from the beginning by the writings and teachings of his predecessors and colleagues, and it is neither possible nor desirable to trace every idea one holds to its original source.

I must, however, express special indebtedness for the inspiration I have derived from the writings of G. G. Simpson and G. R. de Beer, and from discussions with Kenneth Cooper and Norman Newell. For critical reading of these pages and suggestions for their improvement I am grateful to Drs. Ernst Mayr, G. G. Simpson, P. E. Raymond, and Otto Haas.

My research, of which the present paper is a partial outgrowth, has for the past two years been supported by a grant from the Milton Fund of Harvard University.

Homeomorphy

Preliminary discussion. Homeomorphy (Buckman, 1895, p. 456) describes the situation where two not closely related animals look much alike, or where representatives of particular stocks of animals have attained or maintained strong superficial similarity following earlier divergence of the radicles involved. It may be defined as the phenomenon of general superficial resemblance, with dissimilarity in particular significant structural detail.

To the layman the similarities between a porpoise and a shark, or between ordinary types of pelecypods and brachiopods, would indeed seem homeomorphous, but Haas and Simpson (1946, p. 340) have given greater precision to the term by specifying that the similarity between the organisms considered must reach "such a degree that . . . the one may be mistaken for the other even by a trained naturalist." I prefer to employ the term homeomorphy only to designate similarity between the external forms of whole organisms, rather than of particular structures, and also to regard it as properly descriptive of certain instances where the nature of the similarity between organisms is such as to be misleading to the naturalist observer even though degree of resemblance itself may not really be very great.

The general sense of the term is that it denotes the existence of similarity that may be a legitimate source of taxonomic confusion. In this sense the degree of similarity demanded tends to fall with increasing remoteness of relationship.

According to my concepts the most appropriate use of the term homeomorphy implies reference of the groups involved to different subfamilies or larger categories. It has also been applied to instances of striking external resemblance between different genera of the same subfamily. But species or subgenera of the same genus are not in any circumstance properly described as homeomorphous.

Homeomorphy in any sense is rampant among the Brachiopoda. Shells of closely similar shapes and patterns of ornamentation were produced at the same time or different times by brachiopods of varying degrees of relationship to one another. In some instances these shells differ only in particular internal structures; or in one shell being perforated by numerous tiny tubules known as puncta, whereas the homeomorph might be a solid or impunctate shell. A few examples that happen to be convenient will serve for illustration, but many others of equal validity and degree could be presented.

Tetractinella vs. Cheirothyris. A remarkable example of homeomorphy is found between species belonging to two distantly related genera of brachiopods that lived in different times of the Mesozoic Era in Europe (Cloud, 1941). The shells of *Tetractinella trigonella* (Pl. 1, figs. 1–5) and *Cheirothyris fleuriausa* (Pl. 1, figs. 6–12) have such extraordinarily similar shape and ornamentation that they have commonly but mistakenly been regarded as belonging to a single species. Actually the stocks to which these shells

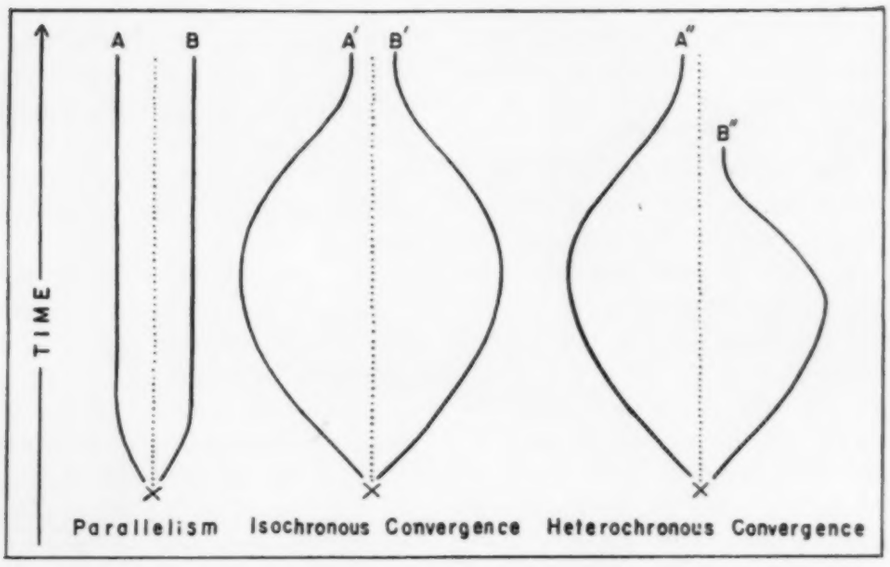

FIG. 1. Schematic representation of patterns of parallelism and convergence. In each instance x represents a theoretical common ancestor, whereas A-B, A'-B', and A''-B'' represent the homeomorphous or near homeomorphous descendant stages.

belong had been distinct from one another for not less than 180 million years (since Late Silurian at least).

Tetractinella, which lived in Middle Triassic [2] (early Mesozoic) time, had an impunctate shell and on the inside a spirally arranged calcareous filament for the support of its cirrate food-gathering apparatus. *Cheirothyris,* which inhabited the Late Jurassic (middle Mesozoic) sea, had a punctate shell and a loop-like calcareous support for its lophophore. It is not necessary to enter discussion here of the differences between their respective cardinalia. In sum *Tetractinella* belonged to the stock of brachiopods known as spiriferoids, whereas *Cheirothyris* was a terebratuloid. If one examines these brachiopods closely one sees that the shell with the impunctate test and the spiral ribbon, *Tetractinella,* has a smaller pedicle opening (at the beak end) than does its punctate, loop-bearing homeomorph, *Cheirothyris.* But this is more readily noticed upon realization of how different the two genera are in other respects.

Because *Tetractinella* and *Cheirothyris* lived at significantly different times they may be called heterochronous homeomorphs. Had they lived at the same time one might say that they were isochronous homeomorphs.

Parallelism vs. convergence. But homeomorphy involves differences of mode as well as differences of time. Because, under concepts to which I adhere, *Tetractinella* and *Cheirothyris* belong certainly to distinct super-families and perhaps to different orders of brachiopods, they should be considered convergent. Convergence then is an evolutionary process that leads toward or to homeomorphy between stocks that diverged a long way from their inevitable common ancestral root before coming to resemble one another again (fig. 1).

Convergence produces the most strik-

[2] The reader unfamiliar with the geological time scale and stratigraphic column may find them tabulated in any textbook of historical geology. It should perhaps be noted that the same names (e.g. Triassic, Permian) denote both *periods* of time (major subdivisions of an Era) and *systems* of rocks. Early, Middle, and Late as referred to periods and Lower, Middle, and Upper as referred to systems denote conventional major subdivisions; the same adjectives without initial capitals are indefinite or approximate in implication. Eras, the major time divisions, are denoted by "zoic" endings.

ing and remarkable instances of homeomorphy, and it poses some interesting problems. One might, for instance, question that *Tetractinella* and *Cheirothyris* were the results of convergent evolution (in this case probably a fortuitous convergence) and suggest that *Cheirothyris* may represent the independent derivation of a punctate loop-bearing shell from the impunctate spire-bearer *Tetractinella*. It would not be profitable to argue that point here, for I can reply briefly to such a suggestion only by stating that evidence could be adduced to show that it is an improbable one. Other instances thought to represent convergence are open to similar query, of course.

However, the analogous query loses force as the probable convergence of external features between representatives of internally widely divergent groups becomes more involved in pattern and simpler in detail. An instance comes to mind of a heterochronous and probably convergent homeomorphy between genera representing three separate families under two superfamilies of brachiopods—namely *Brachymimulus* of the Middle Silurian, *Camarophorina* of the late Permian, and *Norella* of the Middle Triassic (also *Paranorella* of the middle Permian). These are all smooth, biconvex shells of nearly the same size and shape, with the simple but unusual and thus misleading attribute of having a sulcus on the brachial valve; yet their internal structures are widely divergent.

Homeomorphy also results from parallelism,[3] a word that describes the situation where more closely related types, after diverging from a common root, tend to undergo similar structural changes (fig. 1). Parallelism is a more common producer of homeomorphy as I understand it than is convergence, but homeomorphy so produced is ordinarily more subtle and more difficult to recognize than that resulting from convergence.

An example among the brachiopods of a nearly isochronous three-way homeomorphy that is probably due to parallel evolution is furnished by species of the genera *Pionodema*, *Doleroides*, and *Mimella* and described in an important paper by G. A. Cooper (1930). The example selected for discussion in the present paper is one surely familiar in its general terms to a great many paleontologists. It is that of the subquadrate, wide-hinged, thin-bodied, and radially ornamented brachiopods belonging to the families Stropheodontidae and Strophomenidae, and its essential elements are graphically summarized in figure 2.

Stropheodontidae vs. Strophomenidae. The Stropheodontidae have the normal curvature of thin-bodied brachiopods, the pedicle valve (with overhanging beak) being the convex one and the shell concavo-convex. In the Strophomenidae the curvature is reversed except in the earliest growth stages, the shells are convexo-concave, and the strophomenids are said to be resupinate.

Now it is a matter of record that representatives of these two groups range together through a succession of strata representing something on the order of 100 million years of time, or through essentially all of Middle and Late Ordovician, Silurian, and Devonian time. In general the Ordovician members of both stocks have a smooth or non-denticulate cardinal margin or hinge-line, the Silurian representatives a partially denticulate cardinal margin, and the Devonian ones have a completely denticulate cardinal margin. Some overlap occurs in both directions between the Silurian and Devonian, but apparently not enough to affect significantly the general picture. Further correspondence between these stocks may commonly be found in the relative coarseness of the radial ornamentation, and, al-

[3] Contrary to Haas and Simpson (1946, p. 338) whose definitions of parallelism and convergence in other respects are most appealing. As employed by its original proponent, S. S. Buckman, and by most subsequent students of the invertebrates the term homeomorphy has been very commonly applied to members of parallel series (*see*, for instance, Dunbar and Henbest, 1942, p. 53).

together, few invertebrate paleontologists have not had the experience of being momentarily confused by mixed assemblages of isochronous members of the strophheodontids and strophomenids.

The general correspondence between these two morphologic series is remarkable, but there are actually three possible ways of looking at the resemblances seen: (1) they may be the results of parallel evolution, following initial divergence of the strophomenid radicle from the root stock; (2) there is a possibility that the strophomenids represent a gathering of convexo-concave phenotypes resulting from recurrent mutation toward resupination in the strophheodontid stock; and (3) the ingenious suggestion has been made by Professor P. E. Raymond (oral communication) that some of the reversed pairs are simply "ecological genera" whose convexity depended on the side on which they lay at the bottom, as these shells most probably did, the animal turning up from the muddy bottom at the growing edge of the shell, and the top side, whichever it was, becoming concave.

The peculiarities of some of the isochronous reversed pairs are such as to keep open the possibility that the Strophomenidae may be a composite group. Nevertheless, in most instances differences between these isochronously occurring shells of the strophomenid-strophheodontid series, or in their distribution would appear to rule out the third suggestion, and apparent general continuity of trend in opposite groups would militate against

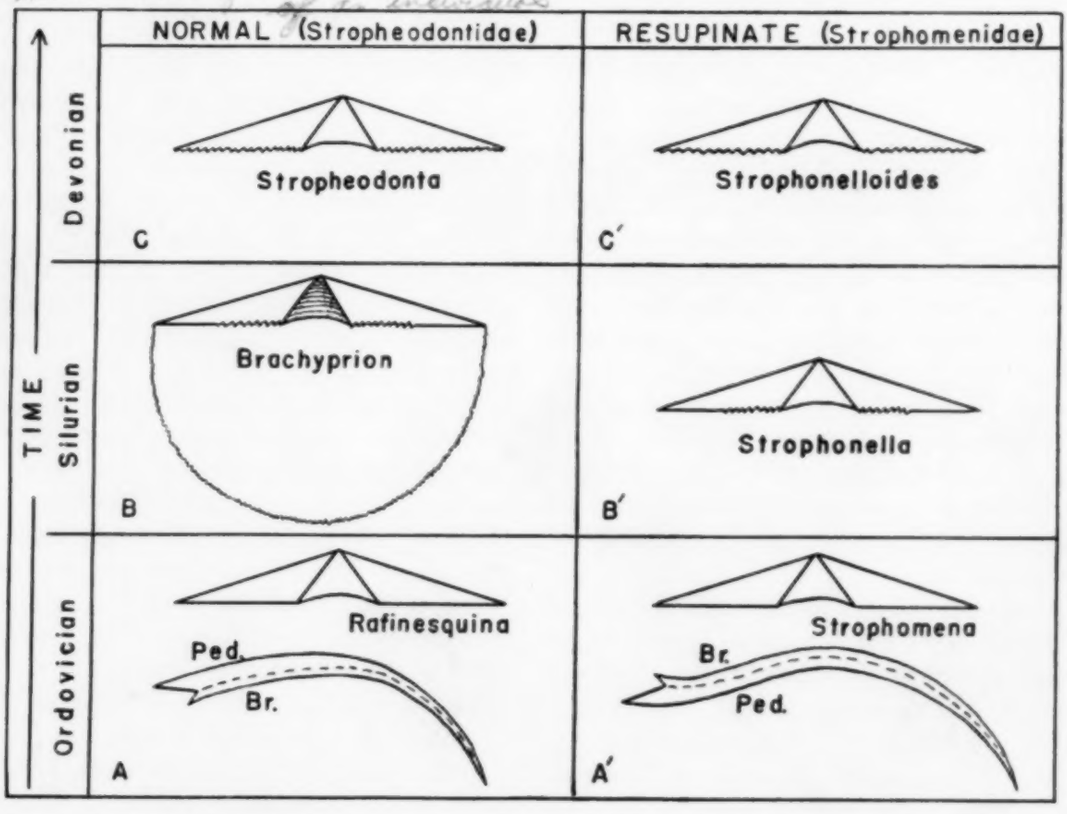

FIG. 2. Gross morphologic sequence in the stropheodontid and strophomenid brachiopods. The part of the shell compared in all boxes is the interarea of the pedicle valve, showing relative denticulation of cardinal margin (hinge-line). The lower figures in *A* and *A'* represent the sagittal profile characteristic of the family in question, the left being posterior, the right anterior. Pedicle and brachial valves are reversed between boxes to show gross similarity of curvature. The figure in box B gives the plan outline of the pedicle valve. The genera cited are common ones at the stages of development indicated, but others would do for illustration and the actual record is much more complex than the diagram indicates.

the second possibility except in certain remarkably distinctive groups such as the Douvillininae, which are not separately apportioned between the normal and resupinate branches anyhow. I think it highly probable, therefore, that the Strophomenidae actually comprises in large part genera that have truly evolved in parallelism with their counterparts of normal curvature in the Stropheodontidae over long periods of time.

In a broad sense, and without troubling to tabulate certain fine generic distinctions, or to record possible instances of prospects 2 or 3 (above), the resupinate line represented by *Strophomena, Strophonella,* and *Strophonelloides* may reasonably be interpreted as having evolved in parallelism with the homeomorphous series of normal curvature represented by *Rafinesquina, Brachyprion,* and *Stropheodonta* (fig. 2). Critical statistical and paleo-ecologic studies will have a bearing on the fine points of this problem.

Basis of parallelism and convergence. In practice, of course, it is commonly difficult to say whether a particular instance of homeomorphy is due to parallelism or to convergence. But, although the results may be very similar, the operative principles behind parallelism and convergence may be very different. Parallelism might be due to direct inheritance of similar but limited patterns of growth in the absence of rigorous selective pressure, as well as to selective effects themselves. But convergence, such as I consider to have produced the heterochronous homeomorphs *Cheirothyris* and *Tetractinella,* can be only fortuitous or adaptive (through selective effects upon phenotypes and thus upon the sorts of genotypes that may persist).

Among extinct invertebrates it is rarely possible to produce strong evidence of adaptive convergence; but there is some good circumstantial evidence of adaptive convergence among invertebrates, and it is so well shown by many vertebrates that one may reasonably assume it to be common. It is also true, however, that fortuitous variation would probably have greater likelihood of producing homeomorphy within a group that was genetically as unelaborate as the brachiopods probably are and were, and among which a relatively limited variety of gross shell form is known. *Tetractinella* and *Cheirothyris,* in fact, probably do represent fortuitous convergence of a remarkable degree.

Instances of probable adaptive convergence. On the other hand adaptive convergence is most likely to be accountable for the fact that certain markedly gregarious brachiopods and pelecypods that thrived in clean and shallow waters of the Permian and Cretaceous seas came to resemble cup-corals so closely that they are commonly taken for corals (Pl. 2). They were all sessile organisms living under closely similar conditions of environment, and they all accumulated an excess of calcium carbonate in a generally similar way.

If even a trained naturalist examined only casually the Permian brachiopods *Prorichthofenia* and *Scacchinella,* the Cretaceous pelecypods *Coralliochama* and *Hippurites,* the operculate Devonian tetracoral *Calceola,* and certain of the more conventional types of Paleozoic cup-corals he might well be uncertain as to which was coral, which brachiopod, and which pelecypod. He might easily take the coral *Calceola* for a brachiopod, group the brachiopods and pelecypods together, and confuse any or all of the brachiopods and pelecypods in question with normal cup-corals. He would be especially likely to do the latter should he see only the conical valves of the brachiopods and pelecypods, and should the corals happen to belong to the Cystiphyllidae, which have an irregular vesicular internal structure remarkably approaching in general appearance that to be seen in the thickened apical ends of certain of the homeomorphous pelecypods and brachiopods in question. In fact trained naturalists have made all of the misinterpretations suggested.

The Permian brachiopod *Leptodus* (Pl. 3), although not actually homeomorphous

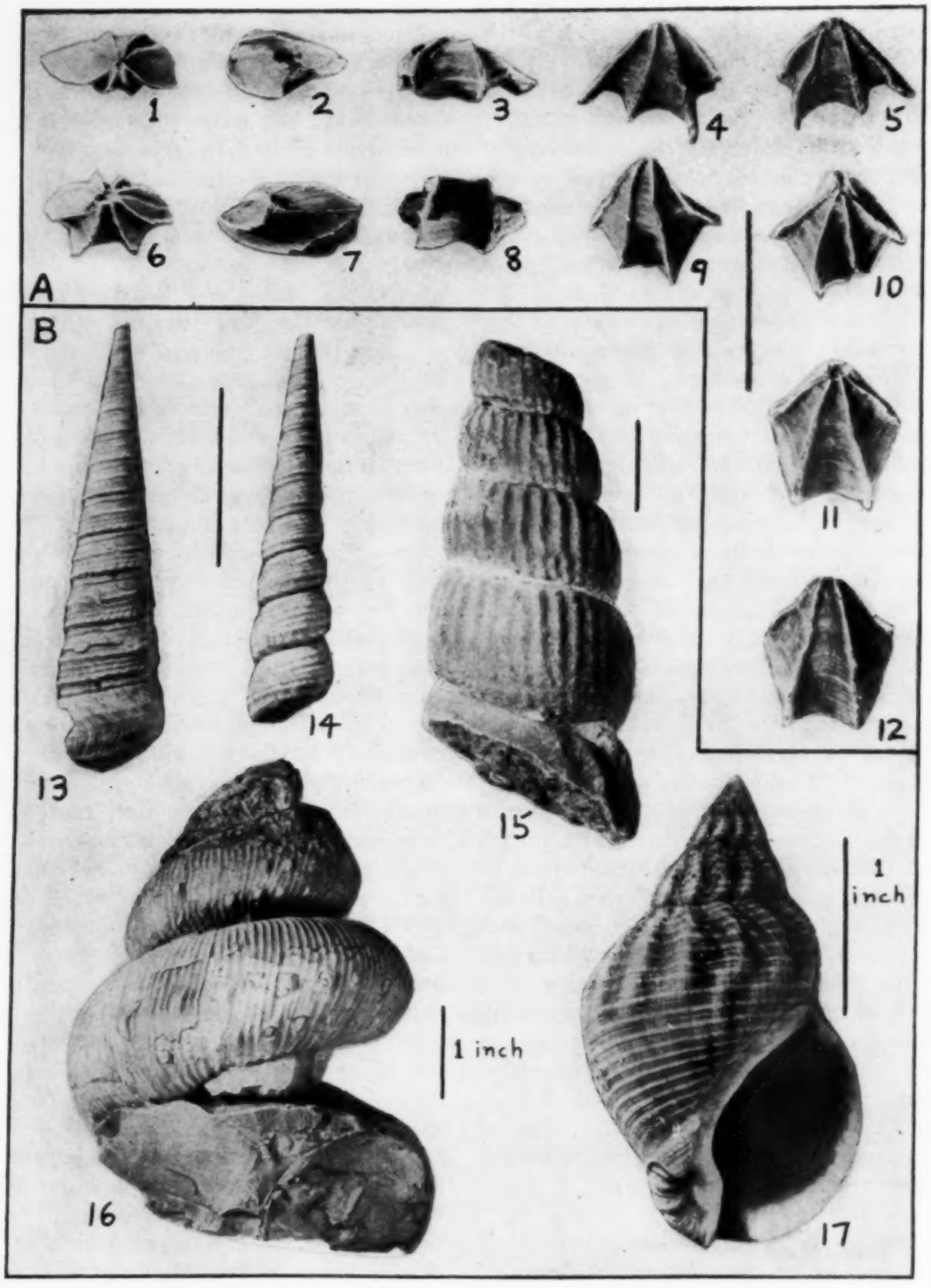

PLATE 1. A. Brachiopod homeomorphs. B. Cephalopods and gastropods.
(The vertical black lines represent 1 inch at natural scale.)

Figs. 1–5. *Tetractinella trigonella* (Schlotheim), Middle Triassic, Recoaro, northwest Vicenza, Italy (Yale collections).

FIGS. 6–12. *Cheirothyris fleuriausa* (d'Orbigny), Upper Jurassic, Leidenheim and Nattheim, Württemberg, Germany (Yale collections).

with the ostreids, had taken on the general habit of growth of oysters long before there was a pelecypod genus *Ostrea,* probably as a result of becoming fitted to a particular ecologic niche—namely one wherein a shell that attached by cementation of a large portion of one surface could get along well. On the other hand, the resemblance of *Leptodus* to the pavement teeth of certain fishes, close enough that it was originally assigned to the fishes by a reputable paleontologist (Kayser, 1883, p. 161), shows that fortuitous or fanciful nonadaptive resemblance does occur.

Helically coiled cephalopods. It is very much of a puzzle to separate cause from effect in contemplating the fact that certain only distantly related cephalopods acquired at different geologic times shells that were coiled in a helicoid spire like a gastropod (Pl. 1), instead of being straight or coiled in a plane as cephalopods normally are. Such situations are found in the nautiloids *Lechritrochoceras* and *Trochoceras* of the Silurian and Devonian respectively, the ceratite *Cochloceras* of the Triassic, and the Cretaceous ammonoids *Turrilites* and *Emperoceras* (irregularly coiled in late stages of growth). The convergence is thus heterochronous between different groups of cephalopods as well as between cephalopods and gastropods.

It has been suggested by Dunbar (1924, p. 203), and it seems eminently logical to suppose, that cephalopods with such snail-like shells were vagrant benthon; crawling about at the sea-bottom as marine snails ordinarily do, instead of being more or less active swimmers (nektonic to nektobenthonic) as cephalopods with straight or planispirally coiled or curved shells (most shell-bearing genera) are for the most part thought to have been. The typically creeping molluscs, the gastropods, normally carry their helicoid shells obliquely, and the aperture of the shell is obliquely situated with regard to its vertical axis. Although some creeping gastropods (*Planorbis*) have an essentially planispiral shell, such a shell is atypical for the group as a whole, and Dunbar (1924, p. 203) has reminded us that "the pelagic gastropods, the pteropods, are all bilaterally symmetrical, and . . . the genus *Atlanta,* which has . . . become adapted to a pelagic existence, is coiled very nearly in one plane."

Whatever the reason, it is a fact that, among animals that have shells, a helicoid shell with an obliquely situated aperture is characteristically associated with a creeping existence. Assuming, as seems probable, that the cephalopods with helicoid shells were persistently benthonic forms, there is no inherently compelling evidence that permits one to say whether the probable association represents adaptive response to a particular mode of existence or whether the helical coil came first, with the creeping habit as a consequent acquisition. Nor can the possibility be eliminated that cause and effect may have been reversed between different cephalopods that acquired helicoid shells at different times. Here, indeed, is a problem requiring further study from large suites of specimens with the proper range in time and with good paleoecologic controls.

Conclusion. Although I prefer to apply the term homeomorphy only to general resemblance of the whole external appearance of distinct animals, it is comparable in a sense to the occurrence of particular analogous organs in distantly related animals. One does not need to be reminded that cephalopods have evolved an eye that resembles and works much on the order of the vertebrate eye (but with a reverse

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Figs. 13, 14, 17. **Gastropods.** *Turritella jewetti* Carpenter and *T. cooperi* Carpenter, Pleistocene, San Pedro, California (HSSC-1599, 1658). *Buccinum undatum* Linnaeus, Recent, Stonington, Connecticut.

Figs. 15, 16. **Ammonoid cephalopods.** *Turrilites costatus* Sowerby, Middle Cretaceous, Escragnolles, France (MCZ-3703). *Emperoceras beecheri* Hyatt, Upper Cretaceous, presumably from Pierre shale of northern high plains in the United States (MCZ-3704).

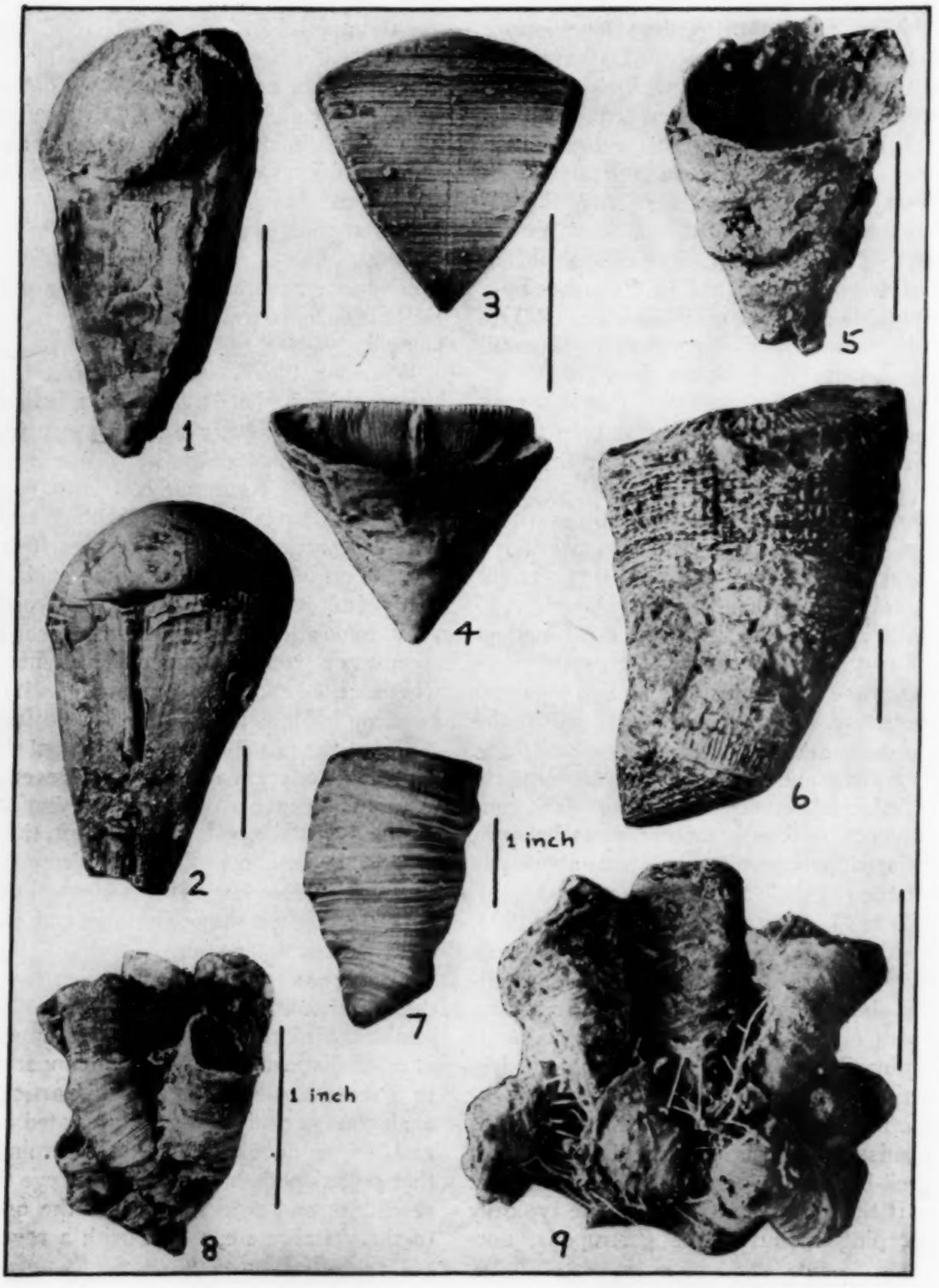

PLATE 2. Brachiopod, pelecypod, and tetracoral homeomorphs.

(The vertical black lines represent 1 inch at natural scale.)

Figs. 1, 5, 9. **Brachiopods.** *Scacchinella gigantea* Shellwien, Permian, Hess fm., Decie Ranch, Glass Mtns., Texas (loc. 46-34). *Prorichthofenia permiana* (Shumard), Permian, Leonard fm., road to Old Word Ranch, Glass Mtns., Texas (loc. 46-27). *"Prorichthofenia"*

mechanism) and is presumably related to an active predatory existence. It is well known that in the case of some of the hermit crabs one or two claws have become modified into the shape of an operculum, so that when they retreat into the abandoned gastropod shell which they inhabit they can block its aperture as effectively as the gastropod did with its operculum. Such features are clearly adaptive, and we may fairly suppose, I think, that, difficult as it may be to prove in extinct invertebrate stocks, homeomorphy commonly results from comparable processes.

It seems reasonable to conclude that homeomorphy has probably resulted more commonly from adaptive convergence or from parallel evolution under similar selective conditions of stocks of similar hereditary background than from fortuitous resemblance. Clearly adaptive convergence is but one aspect of the operative principles of natural selection, and the repeated instances of probable adaptive convergence in many different stocks of animals at many different times are indicative of thoroughgoing selective effects.

Paedomorphosis

Preliminary discussion. Paedomorphosis refers to phylogenetic divergence from some relatively early stage within an ontogenetic cycle such as had previously led to different end results. This concept is perhaps one of the most important in evolutionary theory, for paedomorphosis may well be the mechanism that produced or contributed to the production of the seemingly bridgeless gaps between some major systematic categories. It is, in a sense, a way of building new organisms from old foundations, and of building them by few enough steps and over short enough periods of time that transitional stages are thus paleontological rarities.

The term paedomorphosis was apparently coined by Garstang in 1922 (p. 100), but the general concept involved is an old one, having been formulated at least as early as 1864 by F. Müller (*fide* Hyman, 1940, p. 273). I have not studied in detail the complicated history of the terminology involved in this concept, but paedomorphosis appears to have been used (e.g. Garstang, 1928, p. 62, 134; de Beer, 1940, p. 29, 78 *et seq.*) to mean more nearly what I have in mind to write of than other terms familiar to me (for neoteny, *see* below; for coenogenesis, *see* Hyman, 1940, p. 276, 274, 273). Having accepted the word, the nuances of its past usage will not be debated, other than to comment briefly on the employment of the word "simplification" in Garstang's definition of 1928. Although there may be a simplification in early stages of the process the end result of paedomorphosis is theoretically a reconstitution of adult stages, which may or may not be simplification.

Paedomorphosis, as I shall employ the term, refers to the situation where phylogenetic progression has resulted from the onset of persistent phenotypic (thus genotypic) novelties relatively early in the ontogeny of ancestral radicles. In instances of paedomorphic evolution, if it has not progressed too far, the adult representatives of descendant populations may be expected to resemble in important details the young stages found among ancestral populations. This results from the persistence into the adult stages of the descendants of features that characterized

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uddeni (Bose) King *pars*, Permian, top of Leonard fm., Old Word Ranch, Glass Mtns., Texas (loc. 46-31).

Figs. 2, 6. **Pelecypods.** *Coralliochama orcutti* White, Upper Cretaceous, lower part of Chico series, Todos Santos Bay, Lower California, Mexico. *Hippurites radiosus* Desm., Upper Cretaceous, Senonian, Lameriac, Dordogne, France (HSSC-1433).

Figs. 3–4, 7, 8. **Tetracorals.** *Calceola sandalina* (Linnaeus), Middle Devonian, Germany (HSPC-379). *Heliophyllum halli* Edwards and Haime, Middle Devonian, Hamilton group, Moscow, New York (HSPC-388). *Malanophyllum* sp., Permian, Word fm., Hess Canyon, Glass Mtns., Texas (loc. 46-24).

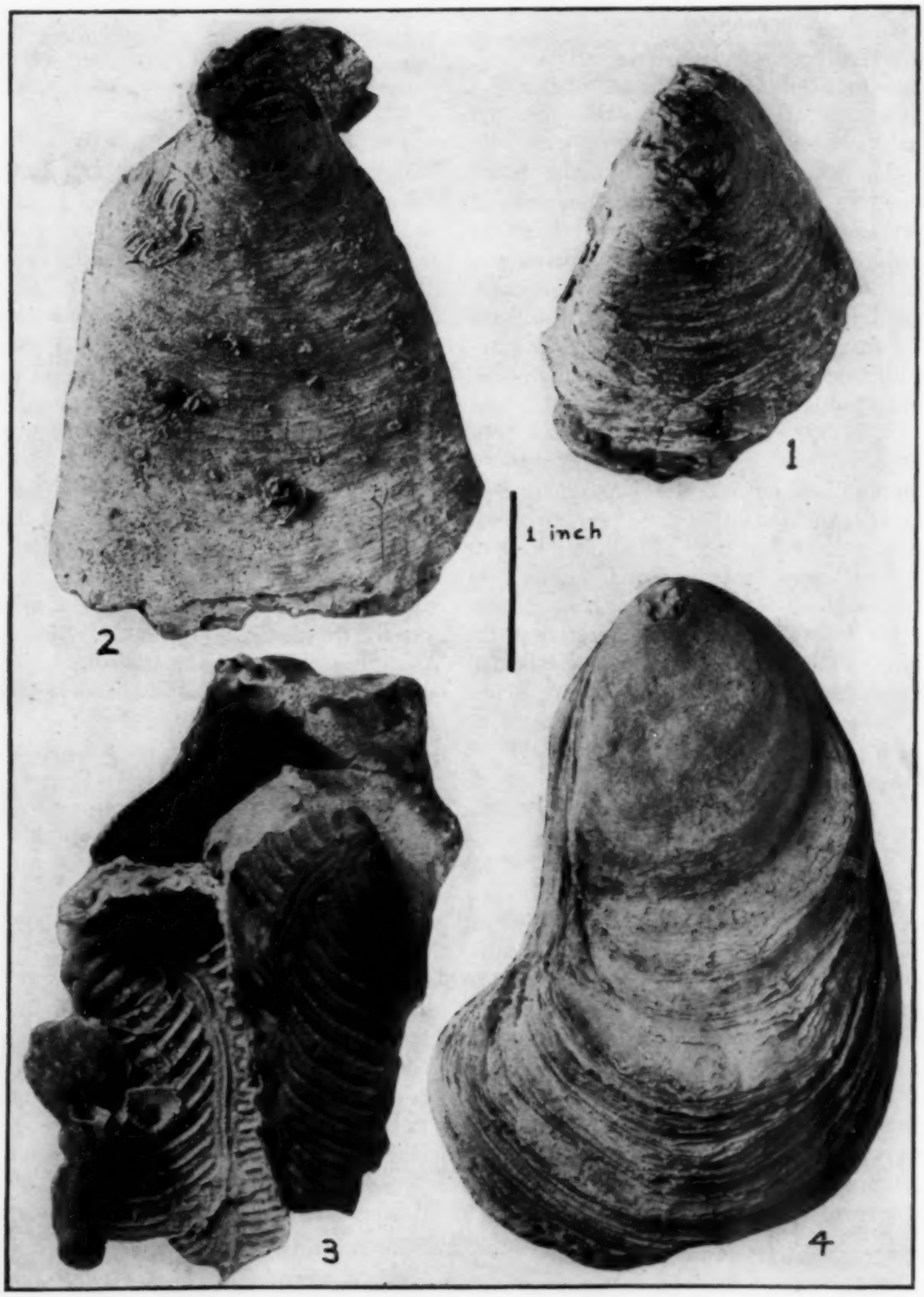

PLATE 3. Brachiopods. *Ostrea.*

(The vertical black line represents 1 inch at natural size.)

Figs. 1, 2–3. **Brachiopods.** *Leptodus* sp., exterior of pedicle valve. *Leptodus americanus* Girty, exterior of pedicle valve and cluster of three pedicle valves from interior

youthful or early ontogenetic stages of the root stock.

Paedomorphosis, in the sense here employed, may be thought of as including three interrelated things. The onset of persistent phenotypic novelties in early ontogenetic stages could result from *intercalation* (theoretically produced by a concordant series of gene mutations), with later ontogenetic stages retained but modified in the descendant population. Or more marked effects could result from *displacement,* wherein the later ontogenetic stages that characterized the ancestral radicle give way to a different late ontogentic succession in the descendant stock. The persistence into a succession of descendant adult populations of features that characterized early ontogenetic stages of the ancestral group seems best described as *phylogenetic neoteny.*

These three factors—intercalation, phylogenetic neoteny, and displacement—are probably interrelated in the production of most paedomorphic trends of persistent phylogenetic significance. Clearly intercalation cannot lead to displacement, nor can displacement very well occur independently, without the interposition of neotenous tendencies. But in theory the latter may and in some instances probably do go so far as to wipe out traces of their action. Such effects could leave "unbridgeable gaps" in phylogeny. The sense of intercalation and displacement are clear, but phylogenetic neoteny requires further comment.

Neoteny [4] in the broad sense of de Beer (1940, p. 46) implies "a *relative* retardation in the development of the body itself as compared with the reproductive glands, so that the body does not run through so many stages in development in the ontogeny of the descendant as it did in that of the ancestor." In this sense neoteny may result from acceleration of sexual maturity (strictly paedogenesis) or retardation of somatic growth (strictly neoteny), and the somatic effects may apparently be either complete or only partial. To be effective in evolution neoteny must be carried far enough to result in the persistence into the adult stage of the descendant population of features that characterized youthful stages of the ancestral radicle. It is thus with an implication of long continued and commonly only partial racial-neoteny that the expression phylogenetic neoteny is used. The concept of variations in the rate of gene action or rate-genes (elaborated by Goldschmidt, de Beer, Huxley) is, of course, helpful to an appreciation of this mechanism.

In discussion it is difficult to maintain consistent distinction between paedomorphosis and phylogenetic neoteny, for the latter is a part of and probably has in most instances a causal or concomitant relation to the former. Thus, in theory, paedomorphosis may result from complete neoteny followed by divergence (Darwin, 1883, p. 86 *et seq.;* Haas and Simpson, 1946, p. 330) through displacement, or by partial neoteny (merostasis) accompanied by intercalation and perhaps eventual displacement, or by phylogenetic neoteny alone. From this it is seen that paedomorphosis may be and commonly is progressive or additive, in some respects at least, whereas neoteny is strictly regressive; and such phylogenetic effects as re-

[4] First described in the Mexican newt *Amblystoma* by the German zoologist Kollman (1882, p. 391). Paedogenesis, epistasy, proterogenesis, and foetalization are essentially synonymous with neoteny in the sense of de Beer, or at least produce similar results, and the shades of implication mean little to a paleontologist. Partial neoteny has been called merostasis by Schultze (*see* Størmer, 1942, p. 153), and in phylogenetic speculation a similar concept has been known to paleontologists as arrested development.

(ladder-like brachial valves missing). All from Permian, Leonard fm., Split Tank, Glass Mtns., Texas.

Fig. 4. *Ostrea virginica* Gmelin. Exterior of right valve. Recent or late Pleistocene, Charles River, Cambridge, Mass.

sult from neoteny alone will be regressive effects.

Apart from its larger implications the concept of phylogenetic neoteny is helpful in understanding some instances of apparent retrogression in evolution. The principle of irreversibility of evolution, or "Dollo's law," is familiar to all, and it appears to be a fact that evolution rarely does backtrack in an established line of descent. But there are striking exceptions to this principle, and these may be examples of phylogenetically neotenous development of the particular structures involved, leading via divergence to paedomorphic results.

Instances that may represent paedomorphosis resulting from phylogenetic neoteny and divergence are to be found in the evolution of those early arthropods known as trilobites, and in the evolution of the stony hexacorals from Paleozoic ancestors.

Trilobita. As regards the trilobites it has long been a puzzle to account for the fact that certain members of the group that appeared first in geologic time went in their ontogeny through a stage similar to that in which many later trilobites remained throughout their adult life. In this stage the facial sutures or "moulting lines" on the upper side of the head shield run out to the sides of the head in front of the genal angles, or cheek spines, if the latter are present. This is called the *proparian* stage—referring to the fact that the moulting lines cut the front of the cheeks. The adults of the majority of Cambrian trilobites had moulting lines that cut the cheeks on the back of the neck and are therefore called *opisthoparian* (proparian trilobites are known as far back as Early Cambrian but were rare before Late Cambrian, and the oldest known trilobites are opisthoparian).

Now it has been shown by Poulsen in 1923, Strand in 1927, and Lalicker in 1935 (*see* Stubblefield, 1936, p. 427; Størmer, 1942) that the opisthoparian trilobites *Peltura scarabaeoides, Sao hirsuta, Olenus gibbosus, Liostracus linnarsoni,* and *Blainia gregaria* ? develop through a transient proparian condition on their way to opisthoparian adulthood. The proparian trilobites attain the proparian state directly and retain it throughout life. It has, thus, been suggested that the facts of trilobite development are best explained "by looking upon adult proparians as permanently neotenous opisthoparians," probably a composite group resulting from the occurrence at diffeernt times of neotenous tendencies among the trilobites (Stubblefield, 1936, p. 431). Moreover, Stubblefield (1936, p. 430) notes that as early as 1909 Jaekel advanced the hypothesis of "arrested development or paedogenesis . . . to explain the . . . condition seen in the facial sutureless members of the families Agnostidae and Eodiscidae (Hypoparian)," where "the trilobite is apparently adult when only a very small number of thoracic segments are formed" —a logical conclusion so far as the known facts of trilobite ontogeny are concerned. These examples of probable phylogenetic neoteny among the trilobites give support to the view that paedomorphosis was a significant *modus operandi* in trilobite evolution and that, as has been recognized by a number of modern specialists on this group, neither the Proparia nor the Hypoparia can be regarded as valid "natural Orders" in the sense of having a monophyletic origin. Evidently these are but stages of development or morphological grades—both paedomorphically attained at different times in trilobite evolution.

Although Størmer (1942) accepts, with emendation, the formerly conventional ordinal arrangement of the trilobites, he recognizes the composite nature of the arrangement and writes of trilobite evolution as exemplifying partial neoteny or merostasis and illustrating (p. 157) "the principle of evolution (paedomorphosis as emphasized by Schindewolf, 1936) according to which a new character appears in the early larval stages and is established in the adult only in later forms."

Stony Hexacorallia. Another example of invertebrate evolution that might represent paedomorphosis is found in the

seemingly sudden appearance early in the Mesozoic (Middle Triassic) of the stony hexacorals or Scleractinia.

It is necessary, however, to precede the discussion with a few explanatory remarks. It adheres to the classification of the Hexacorallia as given by Hyman (1940, p. 371–372) except that I follow Vaughan and Wells (1943) in designating as Scleractinia the corals referred to the Order Madreporaria by Hyman. In keeping with the formerly conventional usage of zoologists and the established usage of paleontologists, the calcareous vertical partitions of the coral exoskeleton are here called septa (sclerosepta of Hyman, 1940, p. 633) and the fleshy interseptal partitions are referred to as mesenteries (septa of Hyman, 1940, p. 539, 603). Relationship of certain members of the Schizocorallia (*see* Shimer and Shrock, 1944, p. 101–103) to the problem discussed is a possibility, seemingly remote at present writing, that should be gone into when relationships, ontogenies, and ranges within this probably composite group are better understood than at present. The Silurian "schizocoral" *Lyellia* has 12 septa, to be sure, but determination of its symmetry awaits ontogenetic study, and it may itself have been a sterile paedomorphic offshoot from some tabulate tetracoral (the Middle Silurian *Cyathophyllum?* illustrated by Carruthers, 1906, Pl. 9, fig. 7, shows almost perfect hexameral symmetry in an early ontogenetic stage). In any event transitional stages to stony hexacorals should be late Paleozoic or earliest Mesozoic (which Silurian is not) and show reduction of tabulae (which *Lyellia* and other "schizocorals" do not but many tetracorals do).

Finally it is to be remarked that a paleontologist is apt to think of the order Scleractinia as practically synonymous with the subclass Hexacorallia (only the Scleractinia and perhaps the Actinia are known as fossils) and that most of the earlier discussion of hexacoral origin has gone on the tacit assumption that this would be understood. The Hexacorallia as recognized are a diverse enough group (*see* Hyman, 1940, p. 640 and preceding) that it is well to emphasize that the present discussion is concerned primarily with those that secrete calcareous exoskeletons —the stony hexacorals or Scleractinia.

Now although most of these corals are colonial and secrete calcareous exoskeletons of complex structure, they habitually begin skeletal growth from the basal disc of the first individual corallite with the secretion of six primary vertical partitions, or septa, radially arranged (schematically shown by fig. 3-B, from Duerden, 1904, p. 81). The regular sorts ideally add new vertical partitions or septa in nearly but not exactly cyclical multiples of six (fig. 3-C; *see* also Duerden, 1904; Vaughan and Wells, 1943), secreted by the epidermis (ectoderm) within intermesenterial inward and upward infolds of the entire body wall. The fleshy vertical mesenteries themselves, of course, are infolds of gastrodermis (endoderm) and cellular mesoglea only, but they too are typically arranged in multiples of six ("more rarely, and then secondarily," pentameral, heptameral, or octameral; Vaughan and Wells, 1943, p. 100). All of the modern reef-building corals belong to the stony hexacorals, although only a few of the living ones are simple cup-like or conical forms.

To follow the record into the past, it appears that the oldest stony hexacorals known with certainty (Middle Triassic, *see* Vaughan and Wells, 1943, p. 69) also add their septa in sextants, essentially as do the Recent ones. But, preceding them in time and ranging through the Paleozoic from the Middle Ordovician on, the sorts of corals that are most like them in other respects, the tetracorals (known only from their calcareous skeletons), add their septa in quadrants.

Remarkably enough, however, the tetracorals early in their ontogeny acquire six primary septa, essentially as do the stony hexacorals—not all at once but as in figures A to D of Plate 4 (after Carruthers, 1906, p. 359, Diagram A, Pl. 9).

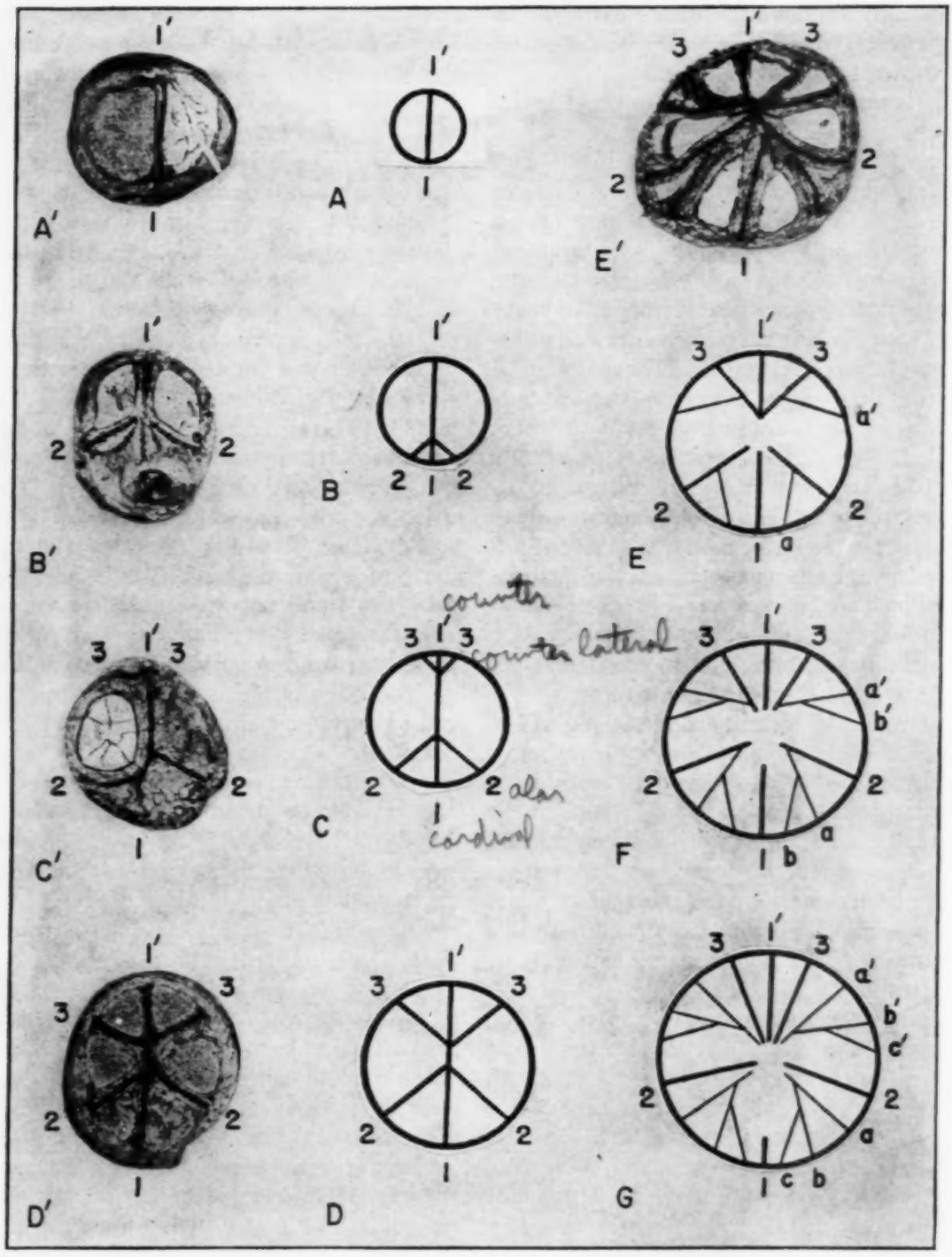

PLATE 4. Sequence of septa in a solitary Tetracoral.

Figs. A-D, A′-D′. Development of the primary or protosepta (1-cardinal septum, 1′-counter septum, 2-alar septa, 3-counter lateral septa).

Figs. E-E′, F, G. Development of the secondary or metasepta.

Figs. A′-E′. Transverse thin-sections of *Hapsiphyllum phillipsi* (Edwards and Haime), Carboniferous, Scotland. Magnification of A′ is × 32, B′-E′ are × 28. From R. G. Carruthers, 1906, Pl. 9.

After the three primary pairs of septa are established in their hexameral disposition there is a pause in septal insertion; and, during or immediately following this pause, septa 1 and 1′, heretofore united, become distinct. Following the initial pause in septal insertion the third primary septal pair is, in effect, shifted toward septum 1′, and septa (a, b, c; a′, b′, c′) are added between the primary septal pairs marked 3 and 2, and between pair 2 and septum 1 in regular succession from pair 3 and pair 2 toward 1, *in quadrants*. No septa are inserted in the segments at first defined by septum 1′ and the septal pair marked 3; and, with development, pair 3 comes to lie closely adjacent to septum 1′, and these segments may be considered to have become aborted. R. G. Carruthers, to whom we owe the best account of septal succession in the tetracorals, convincingly documented by photographs of thin sections (*see* Pl. 4), states that in all the tetracorals examined by him "the septa were found to appear in the same order and manner in both early and late Paleozoic forms" (Carruthers, 1906, p. 358). Peculiarities in the septal pattern of the tetracorals are found in the temporary continuity of the initial septal pair (1, the cardinal septum; 1′ the counter septum) and the fact that the secondary septa impinge basally on pair 2 (the alar septa) and septum 1 in apparently all tetracorals, and distally on pair 3 (the counter-lateral septa) and pair 2 in many. Septal impingement of a different sort, however, is seen in certain stages of development of stony hexacorals (Duerden, 1904, figs. 4–7, 9, pp. 85–90).

If one adheres to concepts of Haeckelian recapitulation or actual irreversibility of evolution the relation between the stony hexacorals and tetracorals is indeed perplexing. Under such views the hexacorals should be the ancestors, or at least both hexacorals and tetracorals should have sprung from a common ancestor. Hope of rationalization came in 1912 with H. L. Clark's (Science) suggestion that one of the soft-bodied organisms, *Mackenzia*, from the well-known Middle Cambrian Burgess shale of the Canadian Rockies in British Columbia might be a naked anthozoan polyp. Further study of the same specimens of *Mackenzia* by A. L. Clark led him to the much bolder conclusion that it is so similar in visible details to the living naked anthozoan *Edwardsia* (A. H. Clark, 1913, p. 507) that "it seems necessary to assign it to a position in the Family Edwardsiidae" (referred to the actinian hexacorals).

As a consequence, in 1921, P. E. Raymond advocated the view that the common ancestors of both hexacorals and tetracorals were *Edwardsia*-like actinians (with the primary scleractinian complement of eight mesenteries), such as might theoretically be represented by *Mackenzia*. According to this hypothesis the tetracorals diverged from the ancestral stock and adopted the habit of lime-secretion early in the Paleozoic (the oldest known tetracorals are Middle Ordovician). Then, having become adapted to an environment of warm waters, they were killed off as a result of a hypothetical lowering of temperatures at the end of the Paleozoic. At this time the naked descendants of *Mackenzia*, having bided the while in cooler waters, were able to spread widely; and, when the waters warmed up again in the Middle Triassic, certain offshoots from the actinian stock took up the habit of lime-secretion and became hexamerally symmetrical scleractinians (stony hexacorals).

Raymond's position regarding the hypothesis of divergence of hexacorals and tetracorals from a common ancestor was logically put and well defended. More-

Figs. A-G. From Carruthers, 1906, Diagram A (p. 359). Drawings schematic and not alleged to be based on any particular tetracoral, but here paired with corresponding photographs. [In addition to specimens here refigured, Carruthers also illustrates a Middle Silurian (Wenlock) *Cyathophyllum* (?) in stage D (his Pl. 9, fig. 7).]

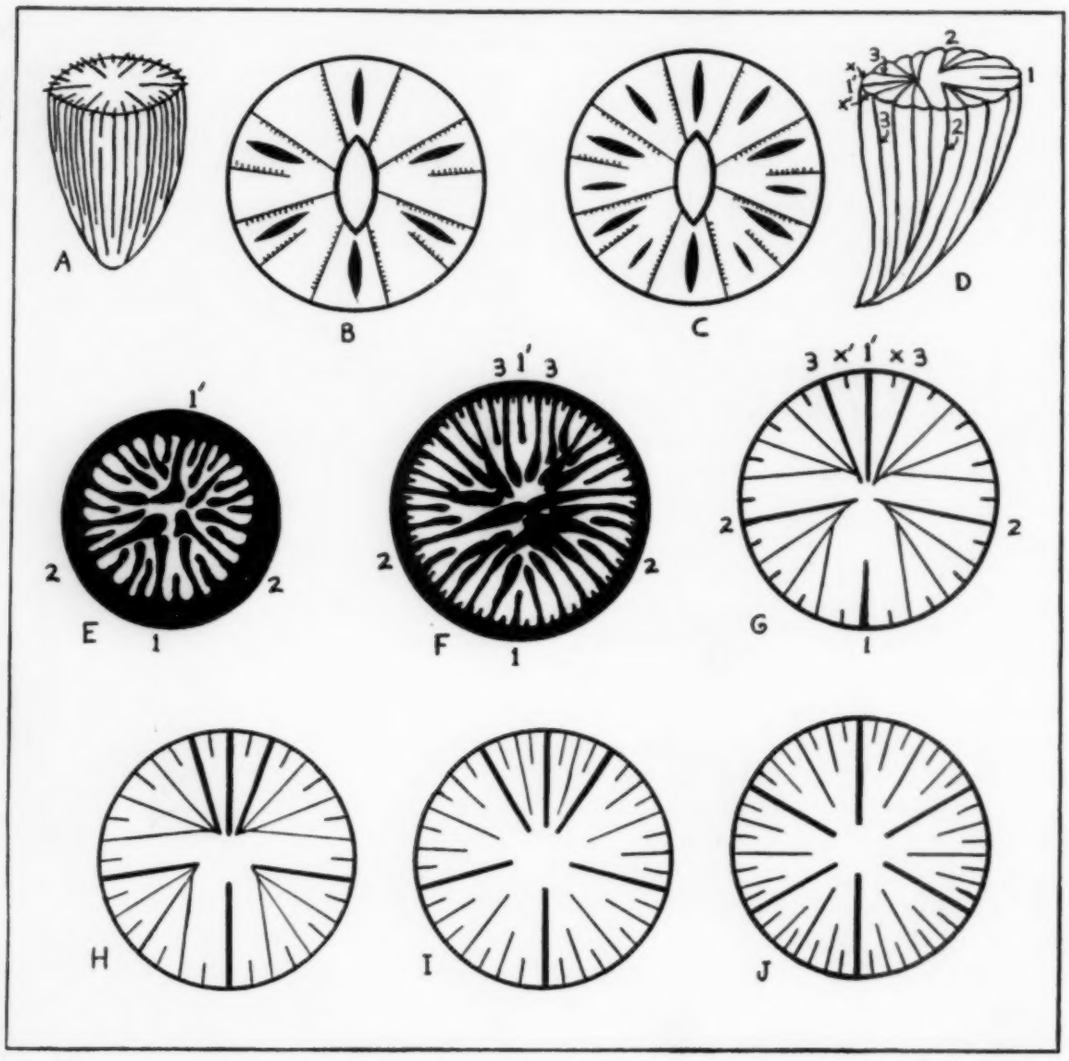

FIG. 3. Septal patterns in tetracorals and stony hexacorals.

A. Sketch of a generalized solitary scleractinian (stony hexacoral) to show hexameral arrangement of septa and subparallel arrangement of exothecal costae.

B, C. Schematic representation of transverse sections of first and second cycle septa in the scleractinian *Siderastrea radians* Pallas, after J. E. Duerden (1904, figs. 1, 2). The black spindles represent septa; the straight lines are mesenteries, hatched on the muscular side; the central portion is the gullet.

D. Sketch of a generalized tetracoral to show tetrameral arrangement of septa and pinnate convergence of exothecal sulci on alar (2) and cardinal (1) septa. It is normal for septa to be missing at x and x′.

E. *Polycoelia angusta* Rothpletz, × 6, Permian, Basleo, Timor (transverse section after Gerth, 1921, fig. 10). Although Gerth remarks on the radial arrangement of the septa in this coral he does not indicate the position of the counter-lateral septa. Apparently they are the fourth or second removed from 1′ (the counter septum).

F. *Plerophyllum timorense* Gerth, × 2, Permian, Basleo, Timor (transverse section after Gerth, 1921, fig. 7). Short tertiary septa are here inserted between the counter (1′) and counter-lateral (3) septa.

G. Representation of the septal arrangement of a Permian tetracoral from Timor (presumably *Plerophyllum*) showing tertiary septa (x, x′) between counter (1′) and counter-lateral (3) septa (after Gerth, 1921, fig. 11).

H, I, J. Idealized series of septal patterns suggestive of stages in a phylogenetic sequence from a late tetracoral (H = *Hapsiphyllum*, Carboniferous) through an early scleractinian (I = *Hexastraea*, Triassic) to a typical scleractinian (J = *Parasmilia*, Cretaceous).

over, Hyman (1940, p. 639) agrees that "the universal occurrence" in the zoanthidean-actinarian-scleractinian line of "an *Edwardsia* stage" indicates as ancestral to it a small weak anthozoan with eight complete mesenteries arising in successive couples (a common idea among zoologists). She also shows (p. 640, fig. 208) the tetracorals on a different line, deriving from an antipatharian ancestor and related to the Alcyonaria and Ceriantharia.

But Hyman (p. 623) also considers that the mesenterial arrangement of the Zoanthidea (of her zoanthid-actinarian-scleractinian line), although different from other living anthozoans, "somewhat resembles that of the extinct Tetracoralla." And, with reference to Raymond's discussion, it is to be remarked that whereas the lowering of temperatures at the end of the Paleozoic is referred to early Permian (or Pennsylvanian?) glaciation, there were late Permian tetracorals; that the presumably stenothermal reptiles were not affected by the postulated climatic changes at the end of the Paleozoic (Romer, 1945, p. 534); and that Pleistocene glaciation did not wipe out modern stony corals (although it doubtless curtailed their range).

As a logical alternative to the hypothesis of divergence of stony hexacorals and tetracorals from a common ancestor one may consider the possibility of direct descent of the stony hexacorals from tetracorals.

The hypothesis of direct descent of the stony hexacorals from tetracorals is supported by evidence of paedomorphic tendencies in at least four genera of late Paleozoic tetracorals. The observations that lead toward this inference began with the discovery by Gerth (1921, p. 87–94, 140–142) that, among the Permian tetracorals of Timor, certain representatives of the genera *Polycoelia* and *Plerophyllum* (fig. 3; E, F, G) displayed the unusual feature of having one to several later-cycle septa inserted between the counter (1′) and counter lateral (3) septa in the formerly aborted sextants. The hexameral symmetry of *Polycoelia* was said by Gerth to be so well advanced that it differs from modern stony hexacorals primarily in that its septa are inserted as successively appearing pairs as opposed to the more nearly cyclical septal insertion of the latter,[5] resulting in the pinnate arrangement of the septa, and in the occurrence on the exotheca of septal grooves in place of septal ridges (fig. 3; A, D). Subsequent illuminating studies by Schindewolf (1930, *see* especially figs. 12–13, 15) have revealed the occurrence of tertiary septa between the counter (1′) and counter-lateral (3) septa in *Hapsiphyllum konincki* from the Lower Carboniferous at Tournai, Belgium, and in *Lophophyllidium proliferum* from the Upper Pennsylvanian Virgil series at Howard, Kansas.

Thus paedomorphic tendencies are suggested in the latest Paleozoic tetracorals. Certainly the structure of *Polycoelia*, *Plerophyllum*, *Hapsiphyllum*, and *Lophophyllidium*, as interpreted by Gerth and Schindewolf, shows relative prolongment in ontogeny of the primary hexamerism of septal arrangement, permitting later cycle septa to appear in the formerly aborted segments, and this amounts to phylogenetic neoteny as I understand it.

As, moreover, the tetracoral stock apparently disappeared at the end of the Paleozoic; to be supplanted in the Middle

[5] Duerden, 1904, p. 88, points out that in the hexacorals "Beyond the primary cycle of six entosepta, which always appear simultaneously, there is a decided dorso-ventrality in the sequence of the septa of each cycle, which for the most part gives a marked bilateral symmetry to the corallum." And, of course, the directive mesenteries show the hexacoral polyp to be bilaterally symmetrical from the beginning.

The heavy radial lines represent the primary or protosepta in all three diagrams. The sequence is based on the septal arrangements actually seen in species of the genera named and is taken from O. H. Schindewolf, 1930, p. 246, figs. 42–44.

Triassic, if not earlier, by stony hexacorals; it is logical to surmise that this situation may have been brought about by paedomorphosis. Further evidence in support of this supposition resides in the observation by Schindewolf (1930, p. 245–246, 255) that certain of the Triassic hexacorals (e.g. *Hexastraea*) have an imperfectly hexameral septal arrangement reminiscent of the septal pattern of the late Paleozoic tetracorals mentioned above. Schindewolf, himself, considers the hexacorals to have derived from the tetracorals by transition and acceleration (Entwicklungsbeschleunigung); and Kuhn, basing conclusions on the work of Schindewolf and others, holds even more definite opinions on the subject. Kuhn (1939, p. 21) states: "Im Perm . . . schon hier der Hexacorallentypus erreicht wird (*Omphalophyllia*). Die mittlere Trias hat noch einige echte Nachzügler der Rugosen (Tetracoralla) geliefert. Die Hexacorallen wurzeln in den Tetracorallen."

Although I would like to believe Kuhn's assertions, the evidence available to me is not so conclusive. It is true that *Omphalophyllia* (= *Conophyllia*), to which Kuhn refers, is indeed a stony hexacoral and is in fact reported from the Permian of Timor by Koker (Lang, Smith and Thomas, 1940, p. 90). But Dr. Otto Haas, who has checked this reference for me, reports (letter to Dr. Ernst Mayr, June 9, 1948)that "Koker says that she is not quite sure about the genus" and that she gives no illustration of septal arrangement (neither Koker's paper nor Schindewolf's papers from 1940[6] on are available to me on the eve of a prolonged absence from the country). Moreover, Vaughan and Wells (1943), in their splendidly comprehensive monograph of the Scleractinia, make no mention of Koker's report, stating on page 69 of their book that "remains of scleractinians have not yet been found in rocks older than Middle Triassic."

To revert now to Schindewolf's hypothesis of transition through acceleration; the question is what was accelerated? Clearly both tetracorals and stony hexacorals went through an ontogeny to reach the adult stage, and septal insertion in both was a more or less continuous process—probably more nearly continuous in tetracorals than in the scleractinians. What one might more logically infer to have happened, assuming that the stony hexacorals were derived from the tetracorals, is that shifting or "migration" of the counter-lateral septa (3) from their position at stage D of Plate 4 was progressively retarded and finally did not occur at all. A consideration of figures D to G on Plate 4 shows that in tetracorals the counter-lateral septa (3) come to impinge upon, or migrate toward, the counter septum (1'), following the pause in development that represents termination of the primary cycle. In theory they crowd the counter septum (1') so that later-cycle septa do not form between them. In the typical stony hexacorals the primary septa are static in orientation from the moment of their origin. Schindewolf (1930) shows this situation diagrammatically in his figures 42–44 (his top row of diagrams, not here reproduced because sufficiently indicated by positions of primary septa in fig. 3; H, I, J), indicating the late-transitional nature of the Triassic scleractinian *Hexastraea* by representing a partial migration of septa that would correspond to the counter-laterals of a tetracoral, and I infer that "Entwicklungsbeschleunigung" was simply an inadvertent choice of terms. Retardation is more to the point than acceleration, and the example appears to represent paedomorphosis brought about by partial phylogenetic neoteny, and intercalation of the other features that distinguish adult stony hexacorals.

Discovery and study of Lower Triassic corals could, of course, have important bearing on the whole problem of origin of the stony hexacorals; and the speci-

[6] E.g. Schindewolf, O. H. 1940. "Konvergenzen" bei Korallen und bei Ammoneen. Fortschr. Geol. Paläont., **12**, Heft 41: 389–492—Ed.

mens on which Koker based her report of *Conophyllia* ? (*"Omphalophyllia" primula* Koker) in the Permian should be critically reconsidered. It is not a criticism to say that this record is potentially too significant to be accepted at second hand and with the author herself in doubt of its validity. Meanwhile the hypothesis of direct descent of stony hexacorals from tetracorals is supported not only by evidence of phylogenetically neotenous tendencies in the latest Paleozoic tetracorals (de Beer, 1940, p. 46, incidentally notes that ripe germ-cells have been found in larval stages of living actinians), but by the relative positions in time of the two groups, and by the seemingly late-transitional septal growth-patterns of certain Triassic hexacorals.

Admitting that the alternative hypothesis of independent descent has attractive features, the only positive evidence evoked by it, the presence of *Mackenzia*, is as consistent with one hypothesis as the other; and the known distribution of the coral stocks in time requires it to assume that "discovery" of lime-secretion by the hexacorals must have essentially coincided with disappearance of the tetracorals. Even before Gerth's discoveries there were cogent arguments in favor of direct derivation of stony hexacorals from tetracorals, arguments that were effectively summarized by W. I. Robinson in 1917, in a paper that also reviews and cites important work not here discussed (*see* also Schindewolf, 1930). The present discussion contends that the concept of paedomorphosis, supported by evidence from the fossil record, provides a promising approach and perhaps the explanation to this old dilemma in phylogeny.

In any event it appears that anthozoan classification needs revision along lines that will more systematically relate ancient and recent representatives of this class.

Other instances of paedomorphosis. Neoteny (either partial or complete) is an observed process in the development of some recent animals. When applied in a phylogenetic sense to problems in evolution it furnishes a compellingly plausible means, under the broader concept of paedomorphosis, of accounting not only for certain puzzling features in the evolutionary history of trilobites and corals, but in other groups as well. For instance, Schindewolf (1936) has furnished instances of apparently paedomorphic evolution among cephalopods and foraminifera, and Garstang (1922, p. 94, footnote) suggests that blastoids and some cystoids may be "paedogenetic" crinoids. With regard to the latter suggestion, although it is certainly true that the long prior appearance of the basic cystoid stock, as currently understood, precludes the possibility of derivation from crinoids for run-of-the-mill cystoid types, some of the peculiar post-Devonian "cystoids" might actually be neotenous or "degenerate" crinoids. Finally de Beer (1940) cites numerous instances of possible paedomorphosis or phylogenetic neoteny, including the evolution of man himself (from Bolk, *in* de Beer, 1940, p. 481).

"Colonial paedomorphosis." A situation of problematical relationship to the question of paedomorphosis is found in the fact that the first-formed thecae of some ancestral monograptid graptolites show the first indications of trends of thecal elaboration that in theoretically descendant graptolites had advanced toward or to the distal thecae (Bulman, 1933, p. 314, fig. 1). De Beer regards this as exemplifying neoteny, but the process can be considered an example of neoteny only in a rather esoteric sense. If one considers the successive colonies as the units of phylogeny, the phenomenon displayed may be thought of as one of intercalation of new features in the early thecae of the older colonies, followed by progressive phylogenetic advance and eventual displacement of the more ancient types of thecae in even the distal areas of the descendant colonies. This might be thought of as a sort of colonial paedomorphosis, but it is a very curious situation about which it would be desirable to know much

more, and which may prove to require some special designation.

Conclusion. To the student of phylogeny paedomorphosis may be a really enlightening concept. Hypotheses of phylogenetic advance by terminal accretion or overstepping (palingenesis, gerontomorphosis, hypermorphosis) have never been able to account satisfactorily for reversal in evolution, or for the origin of most major phylogenetic lines. But geneticists have shown that gene mutation and new characteristics may appear at any stage in ontogeny. At the opposite extreme from palingenetic change one finds new characteristics that appear early in ontogeny, and the potency of their effects is probably magnified by the secondary influences that they may have on the phenotypic expression of all subsequently acting genetic determinants in the changed internal environment (in a broad sense). If, now, in addition, changes of the rate of gene action result in retardation of expression of former late ontogenetic factors so that the intercalated characteristics can come to dominate and perhaps to displace former late ontogenetic characteristics, a stock may literally be rebuilt from the embryo up.

This would be paedomorphosis at its most effective. This would be a way of making new orders or classes or Phyla of animals. Perhaps it is a reason why, even with the falling into disrepute of "the biogenetic law," [7] comparative embryology has continued to play so important a part in phylogenetic speculation.

Eruptive Evolution

Preliminary discussion. Eruptive evolution is the expression here employed to refer to a relatively sudden breaking out of evolutionary diversification within any group of organisms. The term "explosive" has been used for this phenomenon; but as the so-called explosions may be in process during millions of years and probably did not make a loud noise, it is not an altogether felicitous designation. Even where dealing with the record of half a billion years, something that happened in two or 12 million years is hardly explosive, and the word eruptive—defined by Webster's Dictionary as a "breaking forth from restraint"—is a more expressive term for the phenomenon in question.

Now it has happened commonly in the geologic past that certain stocks of animals have passed through periods wherein they became greatly diversified, and following which their descendant representatives were much less varied. Such instances of eruptive evolution are not uncommon in relatively new stocks before they became stabilized or adjusted to particular environmental niches, but apparently they may occur at almost any time in the history of a group. Some stocks have undergone several periods of eruptive evolution, each preceded and followed by times of lesser diversification, so that their phylogenetic lines appear as a set of fanlike nodes, separated by linear or channel-like internodes.

Simpson (1944, p. 88) has given a vivid word picture of what might transpire at times of eruptive evolution. Suppose, to paraphrase with but slight alteration, that because of excessive mutability, relaxation of selective pressure, onset of paedomorphic tendencies or some combination of these, the variability of a group increases and the specific nature of its adaptations decreases. This might result in a situation where a number of the relatively pliable variants produced would find some advantage in particular environmental conditions differing from those of their ancestral habitat, particularly if a variety of ecologic niches became available at the same time. They might then, in the course of time, come to radiate from the ancestral habitat as a number of distinct lines, any

[7] The expression "ancestral reminiscence" (E. B. Wilson, 1899; Hyman, 1940, p. 276) appeals to me as connoting the elements of truth in this concept, and one may speak of a *principle of ancestral reminiscence* that claims suggestion of affinity between organisms that go through similar ontogenetic stages, without requiring that ontogeny be held indicative of a particular phylogenetic sequence.

proportion of which might enjoy temporary success in available ecologic niches. It is to be remembered, in this connection, that an ecologic niche could be available either because it is empty or so sparsely or ineffectually occupied that to get along in it does not involve keen competition.

Situations similar to that described must have been produced at many times among the marine invertebrates of the geologic past. High elevation of continental masses on a number of occasions in the past, by the best of inferential evidence, resulted in restricted shelf-seas and climatic extremes such as are so common today. Such times, presumably, were ones of increased competition for available ecologic niches and probably times of generally channeled evolutionary patterns among the marine invertebrates. Times of great marine inundation of continents, however, probably resulted in general climatic amelioration along with the development of extensive shallow seas. Such developments almost surely would have led to reduced selective pressures and possibly affected rates of mutation, while at the same time making available to the variety of marine invertebrates produced a variety of new ecologic niches (a generally opposite response might be postulated for land-dwelling animals, although the situation would probably be much more complex). The closest modern counterpart of the great epicontinental seas of the past is the widely inundated asiatic shelf of the southwestern Pacific, where interspersed islands and lesser deeps display a variety of ecologic niches and a faunal variety apparently far exceeding that of the narrower, more normal shelf seas of the present oceans (epicontinental seas include shelf seas at the margins of the continents and epeiric seas upon and within the continents).

For an ideally graphic illustration of eruptive evolution the reader should refer to figure 35 of Simpson's book "Tempo and mode in evolution" (1944), a diagram adapted from the spread of a group of ungulate mammals in South America in Cenozoic time. This diagram is based on what quite evidently are much closer controls than those of the generally similar pattern shown by figure 4 of the present paper, and Simpson's interpretation of it was the initial stimulus to the preparation of the discussion that follows.

The early terebratuloid brachiopods. To illustrate eruptive evolution among the invertebrates it is convenient to take the example furnished by the geologically earliest representatives of a group of punctate, loop-bearing brachiopods known as terebratuloids. The terebratuloids made their debut about 340 million years ago, in the middle of the Paleozoic (Late Silurian), and are the dominant group of brachiopods today. Figure 4 represents the approximate known ranges in time of the earlier terebratuloid genera and their inferred relationships. It shows within the main eruptive phase several marked eruptive nodes that probably coincide with the opening up of new ecologic niches as a result of paleoecologic changes or biotal readjustments or both.

Following the more or less eruptive origin of the terebratuloid stock a few generalized forms drifted along until the latter half of Early Devonian time, when there were two closely spaced intervals of eruptive diversification and deployment (Becraft and Oriskany time). This concluded the prominent eruptive phase, but during the transitional times of the Middle Devonian (early Givetian or Skaneateles time) a fourth though much less conspicuous eruptive node appeared. These times of eruptive diversification produced a variety of different sorts of terebratuloids so diverse that it is necessary to recognize among them 28 genera, most of which include only a few species each. The greatest number of genera in existence at any one time was 12 during the Oriskany epoch.

The main eruptive phase of latest Silurian and Early Devonian time lasted perhaps 10 to 12 million years; and by early Late Devonian time, within perhaps 25 million years from the beginning of eruption in latest Silurian time, the known tere-

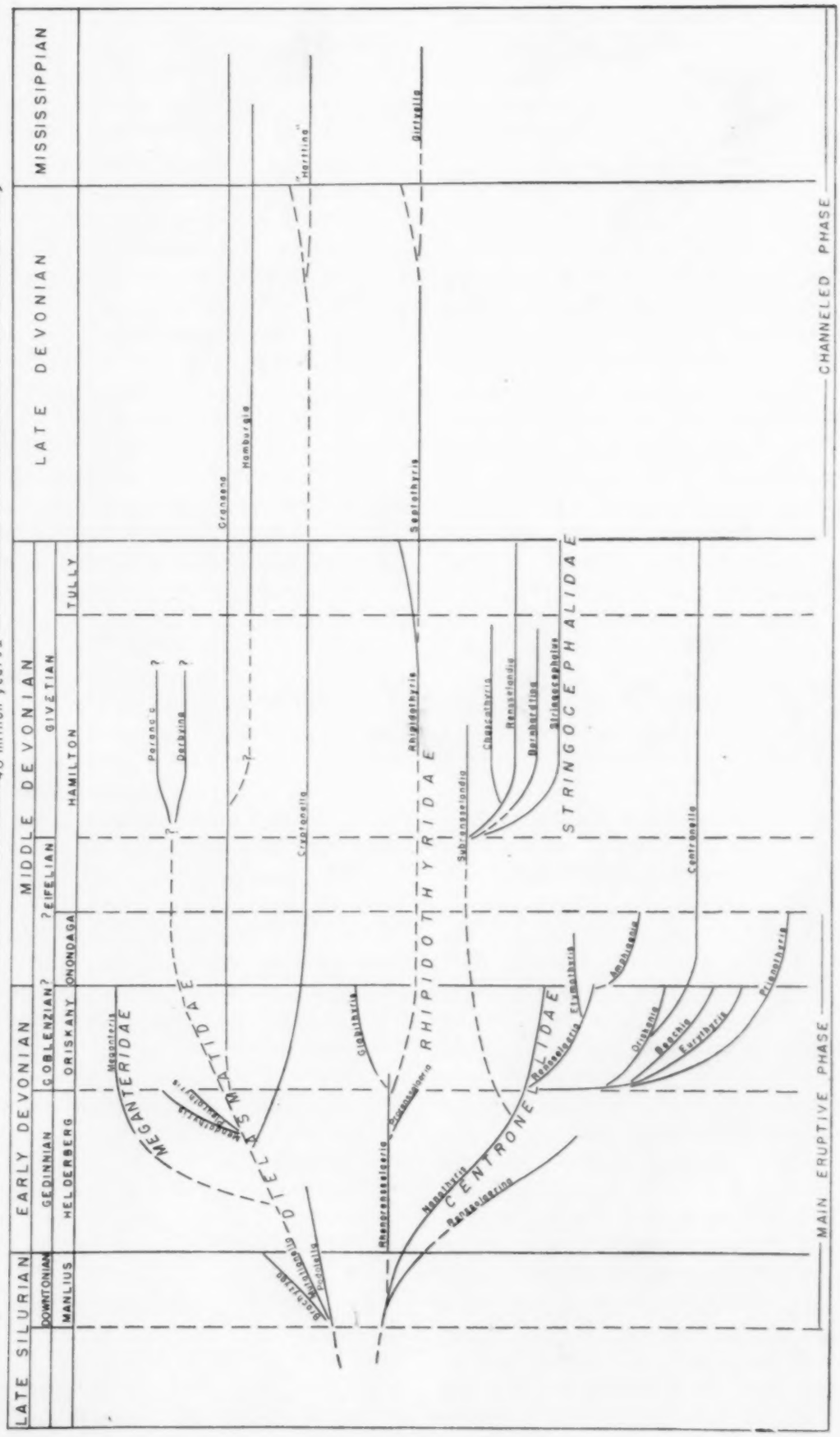

FIG. 4. Eruptive evolution of the early terebratuloid brachiopods.

bratuloids could be included in 3 or 4 genera, all having much the same general appearance.

This picture of eruptive diversification is no figment of the imagination, for really significant diversity has been recognized among these early terebratuloids (Cloud, 1942b, fig. 6). That, moreover, they may in fact have been highly mutable is suggested by the variety of shapes of loop found in what the markedly able Polish paleontologist Roman Kozlowski regards as a single species on the basis of study of 300 specimens, thirty transparent preparations of the brachidium, and a number of serial sections (Kozlowski, 1929, pp. 238–243, fig. 94; *see* also Cloud, 1942b, pp. 116–119, fig. 14). An only slightly less striking degree of variation appears to occur among the loops of some of the early terebratuloids from North America. The form of loop was probably related in part to degree of calcification of the supporting elements of the food-gathering apparatus; but certainly in part also to variation in shape and arrangement of the internal fleshy parts, and in any event very much more unstable in its characteristics than any of the later terebratuloids so far known.

It seems reasonable to infer that the early terebratuloids were highly varied because of excessive mutability or low selective pressure or both. The diverse genera produced apparently spread widely from the ancestral abodes. Following the marked eruptive nodes, and because of increased competition, or for other reasons, selective pressure apparently came more effectively into play and finally only a few general sorts of terebratuloids were able to persist. Although we cannot directly prove adaptive or selective significance on the part of the survivors, such an inference is strongly supported not only by the fact that they did survive when the others died out, but also by the fact that those that did persist were all medium-sized to small, smooth, stoutly lenticular shells of generally similar appearance and that three of the four genera that are known to have persisted into the channeled phase had relatively short and simple loops. Long and complicated loops, although common in the genera of the major eruptive and transitional phases, appear to be rare among post-Middle Devonian terebratuloids.

It might be suggested as an explanation alternative to that of eruptive evolution that the principal evolution of the terebratuloids was going on in the shelf-seas of the continental margins, and that the apparent eruptive evolution resulted from fluctuations in the composition of successively invading faunas. I consider this hypothesis improbable because the pattern seen is so like that of the eruptively evolving endemic South American ungulate faunas as plotted by Simpson (1944, fig. 35); the genera that were especially characteristic of the eruptive period had few species, whereas the most generalized and longest persisting genus considered (*Cranaena*) had many species; and evolution in the shelf-seas should have been more rigorously selective than in the epeiric seas, tending to produce normal phyletic or channeled patterns rather than eruptive patterns.

Other instances of eruptive evolution. The spiriferean brachiopods were undergoing eruptive evolution at about the same time as the early terebratuloids, and eruptive phases are to be seen in the evolution of the productid brachiopods and other brachiopod stocks, probably including later phases of terebratuloid evolution. Although eruption commonly occurs in the presumably plastic early stages of new stocks, it is in fact also commonly delayed until well after first appearances. Eruptive evolution of the sort outlined is common not only among the brachiopods, it has been witnessed in other groups of invertebrates as well. To particularize, classic examples of eruptive evolution may be found among the graptolites, cephalopods, and foraminifera. O. M. B. Bulman (1933, pp. 326–329, figs. 7–9) has emphasized the periodicity of evolutionary diversification among the graptolites, and

eruptive patterns in the evolution of cephalopods and foraminifera are apparent from inspection of their established fossil records. References to "rapid" evolution and short-lived branches are especially common in publications dealing with the late Paleozoic foraminiferal family Fusulinidae (e.g. Dunbar, 1945; Dunbar and Henbest, 1942, p. 53; Henbest in Shimer and Shrock, 1944, p. 19), and a partial interpretive phylogenetic diagram by Dunbar (1940, fig. 9) indicates major eruptive phases of fusuline evolution in early Pennsylvanian and early Permian time. It would seem that the fusulines constitute ideal source material for statistical study of an eruptive pattern.

Inferred general pattern and sequence of eruptive evolution. The point need not be labored here, however, for the inferable general pattern and sequence of eruptive evolution are implicit in the data cited. That pattern and sequence are indicated to be (1) relatively sudden appearance of marked variability; (2) probable availability and proximity of a variety of ecologic niches; and, finally, (3) increased selective pressure, resulting in the weeding out of inadaptive or poorly adaptive radicles and leading to a more regularly channeled evolutionary phase for the particular stock involved.

Origin of the Early Cambrian fauna. The concept of eruptive evolution, however, may bear on a still more speculative field of thought. It is well known that one of the great unexplained facts of the geologic record is the seemingly sudden appearance of representatives of a number of the more important Phyla of animals in Cambrian time, previous to which well authenticated types of animal life are not known.[8] Two considerations come to mind in this connection: (1) The appearance of multicellular animal life in the Cambrian is not actually as sudden as it is commonly made to look, but took place over millions or tens of millions of years. By interpolation in the radiogenically determined time scale it appears that the Early Cambrian epoch lasted about 25 to 30 million years; or roughly one two-thousandths of the time elapsed between the beginning of Cambrian and the present moment in time, and one-half to three-fourths as much time as Sir William Thomson once allowed for the total age of the earth. Yet although marine deposits of Early Cambrian age occur over a large part of the world, only 8 or 9 of the 14 to 16 Phyla of animals known as fossils(the larger figures obtain if the Pleospongia and the Graptolithina are considered separate Phyla) are represented in the Lower Cambrian, and the Early Cambrian representatives of these groups are of markedly simple or generalized types. (2) The appearance of diversified multicellular animal life in the Cambrian may actually have been almost as sudden as the record suggests, an instance of eruptive evolution of the root stock of animal life itself.

If diversification of multicellular animal life did not take place until the beginning of the Cambrian or the latest pre-Cambrian there would have been essentially no competitive pressure at this time, and virtually all ecologic niches that multicelled animals could then occupy would have been available. The surface waters of the sea at that time probably contained an abundance of planktonic algae to start the nutritive cycle running, for we have good evidence that algae had been in existence for a very long time before the Cambrian (Fenton and Fenton, 1939; Raymond, 1935, 1939; Cloud, 1942a, p. 368). Under such conditions it seems plausible to suppose that, once diversification was started, the initial multicellular animal life

[8] Raymond (1935, 1939–1947) discusses this situation in a most illuminating manner and admits as *possibly* represented by actual fossils only sponges and "worms." The record of the sponge is a legend. So far as I can learn, C. D. Walcott is the only man who ever claimed to have seen it, and its present exact whereabouts are not known. The "worms" are simple trails, the nature of whose makers is unknown. Other problematica, such as alleged jellyfish, are of the most doubtful nature.

might have evolved eruptively. If, in addition, perhaps as a result of not yet stabilized sexual patterns, paedomorphic influences should have been common in the early multicellular stocks, it is not too much to suppose that a diversity as marked as that of the Early Cambrian faunas might have been produced within a few tens of millions of years or less.

A somewhat comparable development may be found in the seemingly abrupt ordinal diversification of the mammals early in the Cenozoic, following the extinction of the great reptilian tribes and the resulting availability of a variety of ecologic niches either formerly barred to the mammals by reptilian occupation or nonexistent in fact (Romer, 1945, fig. 257, pp. 325–326; Simpson, 1944, fig. 16, p. 106).

Plausible alternative hypotheses so far suggested are variations of the theme that animal life before the Cambrian was really highly diversified, but without protective covering, and that animals first began to secrete shells at the beginning of the Cambrian (inimitably reviewed by P. E. Raymond, 1935, pp. 385–391; 1947, pp. 33–39). Certain questions come to mind with this suggestion. For instance, why, after extensive and intensive search, have authentic soft-bodied pre-Cambrian animals nowhere been found preserved, as jellyfish and delicate worm-like animals of later times are at some places preserved? This is by no means a fatal point, but it demands consideration, and a hypothesis that gets around it, or in some logical way minimizes it, is stronger than one that asserts that the animals were there in abundance but simply haven't been found, or were ruined by metamorphism, or are not to be had because all known pre-Cambrian sediments are non-marine (a gratuitous assumption). The pre-Cambrian, after all, lasted three to five times as long as the time elapsed since then, and unmetamorphosed pre-Cambrian sediments are not the rarity they were once supposed to be. Admitting that preservation of soft-bodied organisms at any time is a rare occurrence, known instances of such preservations are common enough that it is certainly remarkable that none should be found in the pre-Cambrian, had burials of an abundant and diversified fauna occurred in available sediments.

Other considerations are to be faced. How could an arthropod like a trilobite have evolved the complicated system of muscles that must have been needed to move its many, long, jointed appendages except concommitantly with the development of some sort of skeleton (in this instance an exoskeleton) to attach them to and to produce leverage with? Or how could a brachiopod develop its familiar musculature except in connection with a shell of some sort? Annelids, to be sure, manage their short parapodia quite well without an exoskeleton, and various other wormlike animals have elaborate muscle systems of their own special sorts, as do nudibranchs and some other gastropods (which have probably descended from shell-bearing ancestors). However, an animal such as a trilobite, with long appendages to move, needs a leverage system such as is furnished by attachment of muscles to a test and proper apodemes, and would probably not develop as such without a shell. The muscles of a brachiopod are used solely for opening, closing, and shifting its valves and for rotating on the pedicle; and a brachiopod without a shell would simply have no use for his familiar muscles, would have nothing for them to lever against if he did have them, and could really not be expected to be a brachiopod at all in any recognizable sense.

My lack of ability to encompass the various theoretical biochemical factors that might bear on the foregoing discussion is regrettable. However, some conclusions of the Irish biochemist E. J. Conway (1945) are of more than incidental interest in this connection. Conway (1945) has found a peak of over-restoration of potassium from the ocean to shales "in Cambrian time and probably for some fraction of pre-Cambrian time" (p. 596). This he has thought to be most probably related to "the presence of organic life

with cellular development similar to that now observed, but reaching relatively large volume only at some time in the late pre-Cambrian."

Although its causes are but inferential, the process of eruptive evolution is demonstrable, for its effects may be seen. It seems inescapable that the concept should be brought to bear on speculation concerning that most puzzling of all paleontological phenomena—the relatively sudden appearance in Cambrian rocks of the remains of diversified multicellular animals. An objection to the suggestion here proposed is the fact that it calls for eruptive divergence at an unprecedented scale; although probably by no means such large steps as modern modal representatives of the Phyla in question might seem to indicate, and to some extent approached by Cenozoic mammalian evolution. Moreover, if any time in the past would have favored large-scale eruptive diversification, it may well have been the same as or soon after the first differentiation on earth of well-marked types of multicelled animals.

Considering the available evidence it seems reasonable to entertain the hypothesis that the diversification of the Early Cambrian faunas may be in large part a matter of eruptive evolution. Probably there was a history of pre-Cambrian soft-bodied multicelled animals, but under the concept of eruptive deployment it may have been much shorter and much less extensive than is supposed in conventional theory.

Summary

This paper considers certain phases of homeomorphy, paedomorphosis, and eruptive evolution, with illustrations drawn from the fossil invertebrates.

Homeomorphy. Homeomorphy is the phenomenon of general superficial resemblance, with dissimilarity in particular significant structural detail. The term is employed only to designate similarity between the external forms of whole organisms, reaching a degree or being of a nature such as may mislead even a trained naturalist. Homeomorphy involves differences in both time and mode, and may result either from convergence or from parallelism. The discussion is illustrated with examples from the brachiopods, pelecypods, cephalopods, and corals.

Paedomorphosis. Paedomorphosis refers to the situation where phylogenetic progression has resulted from the onset of persistent phenotypic (thus genotypic) novelties relatively early in the ontogeny of ancestral radicles. In instances of paedomorphic evolution the adult representatives of descendant populations may resemble in important details the young stages found among ancestral populations. This results from persistence into the adult stages of the descendants of features that characterized youthful or early ontogenetic stages of the root stock. Paedomorphosis includes three interrelated things—intercalation, displacement, and phylogenetic neoteny. In theory the latter may go so far as to wipe out traces of its action.

Paedomorphosis is a way of building new organisms from old foundations. It may well have produced or contributed to the production of the seemingly bridgeless gaps between some major systematic categories. The evolution of major morphologic grades among the trilobites and corals is considered from the standpoint of paedomorphosis, and it is concluded that this concept offers a way of comprehending certain anomalies in the sequence of these grades.

Eruptive evolution. Eruptive evolution is the expression employed to refer to a relatively sudden breaking out of evolutionary diversification within any group of organisms. The inferred pattern and sequence of eruptive evolution are (1) relatively sudden appearance of marked variability; (2) probable availability and proximity of a variety of ecologic niches; and finally (3) increased selective pressure, resulting in the weeding out of inadaptive or poorly adaptive radicles and leading to a more regularly channeled evo-

lutionary phase for the particular stock involved.

The phenomenon is illustrated by the evolution of the earlier terebratuloid brachiopods, and the discussion then leads into the highly speculative problem of origin of the Cambrian faunas. It is argued that if diversification of multicelled animal life did not begin previous to the Cambrian or the latest pre-Cambrian there would have been essentially no competitive pressure at this time, and virtually all ecologic niches that multicelled animals could then occupy would have been available. It is proposed as an hypothesis that the diversification of the Early Cambrian faunas may be in large part a matter of eruptive evolution, most nearly comparable to the seemingly abrupt deployment of mammalian stocks in Cenozoic time.

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THE METHODS OF COMPARATIVE ANATOMY AND ITS CONTRIBUTION TO THE STUDY OF EVOLUTION

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Renewed interest in problems of phylogeny and evolutionary mechanisms characterizes the achievements of the 20th century biologists. A considerable number of synthetic works have been written in the past few years, all of them ultimately concerned with transformations within the structural design of the organism. Thus, it should rightly be expected that morphology, the biological discipline that occupies itself especially with organismic form, should play an important role in the discussion of such theoretical problems as phylogenetic progression and the mechanisms that bring it about.

This welcome revival of interest in phylogenetic questions has, however, brought forth a considerable amount of confusion in the minds of many biologists as to the methodological procedures and to the limits of morphology, and the particular kind of contribution that this discipline can make to the theoretical discussion. The need for a clarification of morphological concepts has become especially urgent, as is evidenced by an impressive list of publications that are directly concerned with this matter. A survey of these publications readily reveals a great deal of disagreement among the authors with regard to the nature and content of morphological concepts, particularly that of homology. There are essentially two schools of thought represented. On the one hand, morphological concepts are being broadened and transferred from the methodological to the theoretical level (Boyden, 1935, 1942, 1943, 1947;[1] Hubbs, 1944; O. Haas and Simpson, 1946; Etkin and Livingston, 1947). On the other hand, morphological concepts have been further developed within the realm of their applicability—that is, the method of comparative anatomy (Naef, 1913, 1917, 1919, 1921–28, 1923, 1926, 1927, 1931; Jakobshagen, 1924, 1925a, 1925b, 1927; and Kälin, 1933, 1935, 1941, 1945). The work of these authors has either been overlooked, or they are said to be advocating a return to pre-evolutionary thinking (Hubbs, 1944; Haas and Simpson, 1946). This statement, however, does not conform to the facts, as will be shown below, and as is readily confirmed by an examination of the works of these authors themselves.

Since there is much disagreement in this matter among the authors, and in view of the fact that the numerous and important contributions to this subject, particularly by Naef and Kälin, have not entered the English language literature, an attempt is here made[2]

1. to circumscribe the scope of comparative morphology,
2. to restate its basic conceptional foundation and to clarify its fundamental methodical procedures,
3. to analyze its results as to their meaning, significance and limitation, and
4. to indicate the contribution that comparative morphology can make to the over-all discussion of evolution.

For the purpose of initial orientation, it may be helpful to compare the working

[1] Boyden (1943 and 1947) has recently tried to return the concept of homology to the status of a methodological tool and does not agree with Hubbs (1944), Haas and Simpson (1946) or Etkin and Livingston (1947). Boyden's concept, although essentially correct, has the weaknesses of Owen's definition (see below).

[2] Unfortunately, much of the pertinent literature in German is clothed in difficult language and its translation poses considerable problems. The present essay is thus an attempt to state the matter at hand in as simple terms as possible.

process of an experimental science with that of a non-experimental science (fig. 1). The former employs a well-known method, the experiment, which produces factual results that need to be interpreted. The non-experimental sciences also have a method, though not so well known, to gain factual results that need interpretation. This method consists of observation and comparison and the concepts gained from them are usually referred to as the morphological method. In the experimental fields, the two phases of the working process are always clearly separated: the results of the experiment can be clearly distinguished from their interpretation. The very same situation prevails in a non-experimental science such as morphology, but many authors disregard it, thus actually removing the solid foundation from under this discipline. It should be interesting to witness the storm of protest that would ensue among sound experimentalists, if it should become practice to ignore the reporting of experimental data and to present to the reader merely the author's interpretation of his experimental results. Yet this is what is happening in a large sector of the morphological and systematic-zoological literature.

The following essay is devoted to a clarification of the morphological method, following mainly Naef and Kälin (op. cit.), in an effort to clarify the status of the contributions of morphology to the general discussion of evolution in relation to those of other biological sciences. It may again be pointed out that neither Naef, nor Kälin, nor this writer intend to advocate a return to pre-evolutionary thinking, or to suggest that morphological results should be considered as ends in themselves. All of these writers firmly confess to an evolutionary outlook. What is being advocated is a sound morphological method, with which to achieve morphological results that form the basis of sound phylogenetic (evolutionary) interpretation.

Morphology—the Study of Organismic Form

Morphology is the biological discipline that deals with the investigation of the normal,[3] phenotypically expressed structural design of organisms. As such, it is not merely interested in the over-all structural make-up of individuals or groups (topographic and comparative gross anatomy), but also in the microscopic structure (microscopic anatomy), the developmental and geologic aspects of the form-problem (ontogeny, paleontology), and, finally, in questions of functions and envi-

[3] As distinct from the experimental and pathological form conditions.

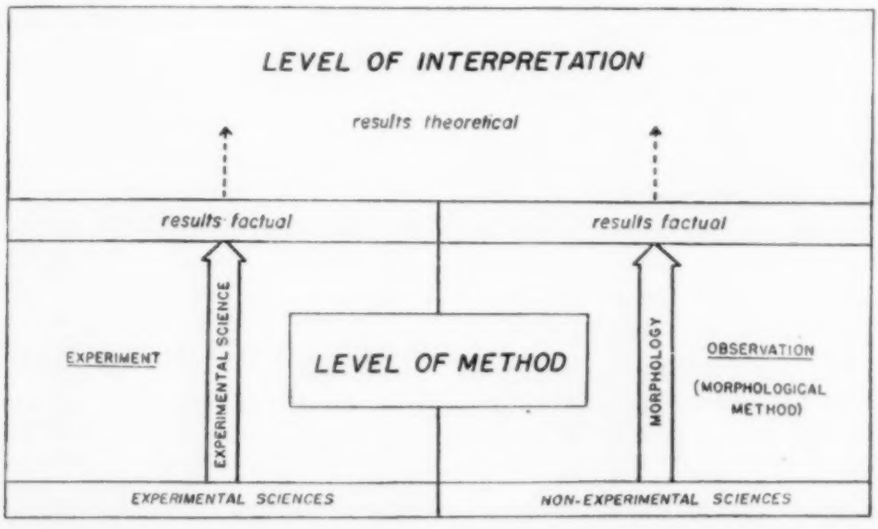

Fig. 1. Diagram to show the main phases in the working procedures of experimental and non-experimental sciences.

ronment in so far as these appear to be correlated with structural design (comparative biological anatomy). In all cases, it is ultimately the form-problem that is of central interest and we must thus consider all these fields as disciplines of morphology.

Since morphology, as here defined, is an utterly non-experimental science, its results can neither be obtained nor rejected on the basis of experimental evidence. If, for instance, somebody should contend (and this has been done) that the ichthyosaurs and the whales, or the flightless birds, the "ratites," are closely related animals, there is no reliable experimetal way of proving or disproving the opinion. In order to interpret correctly morphological phenomena, it is necessary to understand fully the nature of the objects investigated and the methods available for their study.

There are considerable differences in the nature of the objects to be investigated in the various morphological disciplines. It is this difference that has tended to break morphology up into its several subspecialties. Let us suppose that we had had available for study all the organisms that ever lived through the history of the earth, not as fossils, but alive and in their proper surroundings; there would not be any reason for cleaving morphology into a number of specialities, except, perhaps, for purely practical reasons. As it is, only fragments of the over-all morphological record are available. For instance, the entire structural make-up is available only in the organism alive at present; of those of the past, only a part of their bodily organization may be preserved in fossil condition (internal and external skeletons).

The study-objects of comparative gross anatomy, of histology and of organology are thus essentially adult organisms living at the Present. The materials are satisfactory in so far as they permit the study of the complete organism, but they are limited to one epoch of geologic history. The factor *time* enters into the picture, if form-stages are investigated with regard to their ontogenetic development (ontogeny). Ontogenetic development is a continuous process that presents itself to the morphologist as an infinite number of form-stages, illustrating the process, if arranged in their proper chronological order. Thus, the adult form-stage can be viewed in its historic aspects. *Time* in a different dimension is met with in paleontology. Essentially only adult form-stages present themselves in the geological periods, thus depicting the form problem in a different historic perspective.

It is important to keep in mind in what ways the two historic series of form-stages (the ontogenetic and the geological ones) differ from one another. The most striking difference lies in the relationship between any two successive stages in the two series. In one case (ontogeny), we are certain that the second of two adjoining stages of a series has actually developed from the first; this can be observed and confirmed. In the geological series, we are never certain, but can only achieve a greater or lesser degree of probability. There are other differences, of course. One historic, formative process takes place within the individual, whereas the other involves at least successive populations. Comparative biological anatomy (Böker) deals essentially with the same situation as comparative gross anatomy, except that correlations of form with function, and of organism with environment are particularly investigated.

The above considerations should make it clear that comparisons between materials of such different nature (adult recent with adult recent; adult recent with adult fossil; adult recent with embryonic; the latter with adult fossil) rest on different erkenntnistheoretic [4] planes, and thus cannot be evaluated in an identical way. Full clarity in this matter has not yet been achieved, but some attempts at clarification have resulted in the removal of controversies of long standing; see for instance Kryzanowski (1939), who shows among many things that caenogenesis and palin-

[4] Erkenntnistheorie = theory of cognition; a good adjective is not available in English.

genesis exist neither as concepts nor as phenomena.

The Methods of Comparative Morphology

Comparative morphology rests almost entirely upon the fact that there are various kinds of relationships between structures of different organisms (interindividual relations) and within individuals (intraindividual relations), between structures and functions, organisms and environments, etc. These relationships express themselves in various degrees of conformity between the objects considered.

The analytical tool of comparative morphology is, as its name implies, *comparison*. Naturally, any two parts of different organisms or within one individual can be compared with one another. But the erkenntnistheoretic value of such comparisons is greatly different, as an example will readily demonstrate. Suppose the following comparisons be made: the subterminal phalanx of the third digit in the hand of a lizard with (1) the kidney of a cat, (2) the premaxilla of a dog, (3) the subterminal phalanx of the third digit in the manus of another lizard, and (4) the subterminal phalanx of the third digit of the foot of the same individual. An evaluation of the four comparisons reveals that in the first case the structures correspond in two ways; they are both made up of cells (different as these are) and these cells arise ontogenetically from the mesoderm. In the second example, the degree of structural correspondence is considerably greater, both structures consisting of similar cells (bone cells). The degree of correspondence between the elements in the third example is very great: similar cells, similar ontogenetic development (mesodermal, preformed in cartilage), similar position in the body with regard to the organisms concerned, thus also similar position within the manus, arm, anterior part of the thorax, etc. The degree of over-all similarity in the fourth example is also very great, but differing from the third comparison in that the structures do not correspond with regard to the body as a whole.

Some of the structural relationships uncovered by comparative morphology proved of such value that they become important concepts (morphotype, structural plan, homology, etc.), representing fundamental elements of the morphological method. Before discussing the latter, it seems necessary, however, to make one point clear. All morphological concepts express *observed* relations. These relations are facts, verifiable by any subsequent observer. The morphological concepts are factual generalizations derived from observed structural relationships and as such *they do not and cannot carry phylogenetic implications.* The translation of morphological results into phylogenetic terms is a matter that must be judged in each case according to its merits, in terms of greater or lesser degrees of probability. But such procedure is outside the realm of morphology; it belongs in the sphere of theoretical, over-all synthesis of the results of all biological sciences, the discussion of which must not impair the methodological foundation of any of the disciplines. An example to illustrate this matter in all its clarity and simplicity may be drawn from Hubbs (1944). Hubbs writes (p. 301), "Good circumstantial evidence indicates, to take one example from our own studies, that bifid teeth and intestinal coils of a certain type have been evolved repeatedly in the Goodeidae, a family of cyprinodont fishes (Hubbs and Turner, 1939). In the Clupeidae, as a second example, a peculiar type of raker-lined pocket has been developed, again and again, we feel sure, by an extension and evagination from the upper anterior end of the fourth gillslit (Hubbs and Lagler, MS). The end results of such parallel evolution may be scarcely distinguishable on any morphological, physiological or developmental grounds. Are they homologous? On the basis of essential similarities and of mode of development in the individual, we may say 'yes'; on the basis of monophylety, we could say 'no.'"

The morphologist is faced, in the cited example, with the *facts* that bifid teeth and intestinal coils of a certain type occur in several members of the family Goodeidae, and raker-lined pockets are found in various representatives of the Clupeidae. About the phylogenetic history of these organs, he knows, *a priori*, absolutely nothing. The morphologist, however, recognizes that the organs under consideration exhibit a high degree of structural similarity, microscopically, macroscopically and in the structural relation to the rest of the fish body, as well as ontogenetically. Here, then, the morphologist has found a form relationship between organs of different animals that he calls a homology. The relationship thus expressed is factual and merely means that the organs in question correspond in the various species to the degree outlined above. The theoretical discussion as to whether these organs sprang from a common ancestral anlage or had developed independently in different lines can only lead to the suggestion of a greater degree of probability for the one than the other. Obviously, regardless of what the theoretical interpretation may be, the striking form relationship still exists as before, as a homology!

The value of morphological results in the discussion of phylogenetic topics is, however, by no means impaired by the fact that they are not direct keys to such problems. Morphological methodology has many avenues of approach, and indeed, in numerous instances, morphology has amassed enough material to make its phylogenetic interpretation appear as a pragmatic certainty.

Methodological Concepts in Comparative Morphology

The structural plan and the morphotype [5]

The variety of form expression in organisms is potentially infinite, due to differences of structural design of their parts in relation to each other and to the body as a whole, and to the countless form variations that are possible within each basic design. Order may be achieved in this complexity of form by grouping the organisms into a hierarchical system of categories, ascending from the smallest unit in which the common basic design includes the entire structural make-up of the organisms contained to the largest unit in which that design may include only a few structural elements. This procedure is practically expressed and evaluated in the familiar systematic classification of animals and plants.

The conformity to a design in the topographic (spatial) relationship of the parts of an organism to the body as a whole is called the *structural plan*. It represents the basic, mutual arrangement among the parts of the compared organisms. Naturally, in a group of greatly different organisms, the structural plan includes only a few common features; on the other hand, the structural plan of a group of more or less similar organisms is rich in common features (the organisms conforming in many respects to a mutual pattern) but it represents only a small variety of design (fig. 2).

This concept is of great importance, because organisms can be profitably compared morphologically only within the scope of their common structural plan. It is, for example, not possible to regard the structurally similar paired eyes of the squid (as elements of the structural plan Mollusca) and the paired eyes of a vertebrate (as elements of the structural plan Vertebrata) as homologous, because the structural plan of the phylum Mollusca is basically different from that of the phylum Chordata. These eyes can be compared only within the mutual structural plan of both the Chordata and the Mollusca. But, in this greatly abstracted plan, these eyes appear merely as light receptor organs without specific spatial relationships to the organism as a whole, and as such the squid eyes are not only homologous to the paired eyes but also to the parietal

[5] The term *morphotype* is here introduced for the first time. It is the equivalent of the morphological type or *Morphotypus*, as used in German.

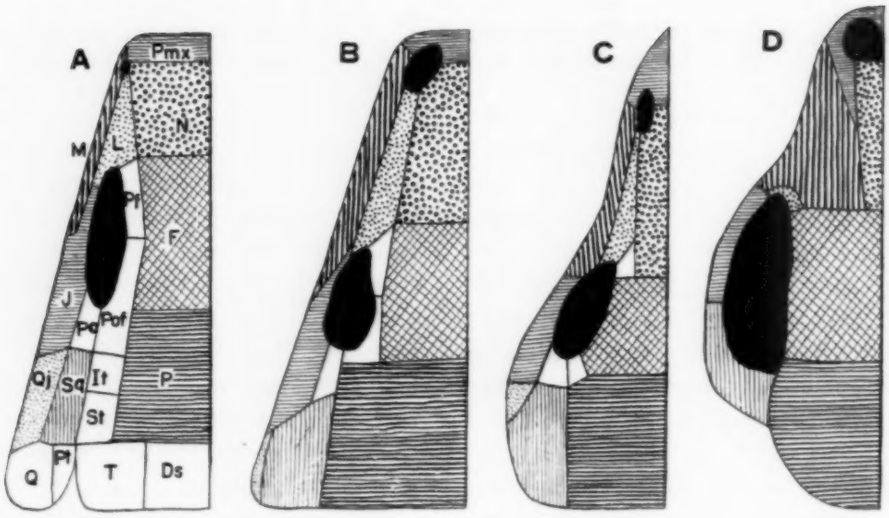

FIG. 2. Illustration of the structural plan of the roof bones of the skull. A, Amphibia; B, Reptilia; C, Aves; D, Mammalia. The figures show the topographic arrangement of these bones with regard to the skull (and the body) as a whole. Condition A may serve as the structural plan for all Tetrapoda.

Pmx premaxilla
M maxilla
N nasal
L lacrimal
F frontal
Pf prefrontal
J jugal
Pof postfrontal
Po postorbital
Qj quadratojugal
Sq squamosal
It intertemporal
St supratemporal
P parietal
Q quadrate
Pt pterygoid
T tabular
Ds dermosupraoccipital

eyes of the Chordates. Hubbs (1944) came essentially to the correct conclusion (as illustrated by his examples), namely, that organismic structures cannot be considered homologous, except within the frame of the common structural plan of the compared organisms. He states (p. 297), "Two characters may be homologous from one point of view but nonhomologous from another viewpoint." The contention that it is a matter of point of view whether structures in compared organisms are homologous or not, "As a vertebrate limb, a bat's wing is homologous with a bird's wing, though as a wing it is only analogous," is not tenable however. The comparison of structures in organisms belonging to groups of different structural plans, rather than their comparison within their mutual structural pattern, inevitably leads to serious methodological difficulties.

The structural complexity of an organism at any time during ontogeny is a product of differentiation during growth. Consequently, as Naef and Kälin have pointed out, the concept of the structural plan is four-dimensional, "Werdeplan," including the factor time. Actually, it is even more complex where fossil materials are involved.

The concept of the *morphotype* is closely related to that of the structural plan. The various parts of living bodies do not merely conform to a basic topographic pattern, but they exhibit, themselves, a great variety of form. In terms of the structural plan, the tetrapod humerus, for instance, is a structural unit in the most proximal section of the forelimb. As such, it consists of cartilage or bone and it appears in a great variety of shapes: different degrees of torsion of the distal against the proximal end; differ-

ences in the relative size, differences in attachment areas of tendons, and in vessel and nerve passages, etc.

The evaluation of form conditions is as relative as the evaluation of sizes. Thus, as Kälin points out, it has long been felt among systematic biologists that there are norms (standards) with which actual form conditions can be compared, in an analogous way as, in the physical sciences, we measure by comparing sizes with standard size units, e.g. the standard meter. In other words, we determine deviations from an established norm.

In morphology, the norm is the morphotype which is an abstraction of the actual form variety within a group of organisms of the same structural plan. It is arrived at by abstraction from the actual form variety within a group (*in praxi*, usually but not necessarily a systematic category) and thus the actual form conditions can be *thought* of as being derived from it. Thus, we can arrive at the familiar morphotype of the skeleton of the tetrapod limb—disregarding all the numerous peculiarities of form in the individual representatives of the group, and including only those features that are unspecialized and mutually present in all—by constructing an extremity consisting proximally of a single, rod-like stylopodium, distally followed by two rod-like elements of the zeugopodium and the latter forming the base of a five-rayed autopodium. From this scheme, we can (ideally) derive the limb skeleton of, e.g., the Equidae in the well-known manner by progressive reduction first of digits 1 and 5, then digits 2 and 4; that of the Cavicornia by reduction of the 1st, then the 2nd and 5th digits and partial fusion of the remaining parts. As applied to a few well known examples, such as the one cited above from Kälin (1932), involving for the most part large systematic categories, most biologists are familiar with the concept of the morphotype. But its applicability and value are equally great in groups of lower systematic rank.

It may be difficult, particularly for the beginning student of morphology, to understand the difference between the concepts of the structural plan and the morphotype. At first, it would seem unnecessary to make a distinction, since at every systematic level the morphotype is associated with a structural plan of equal systematic rank. Closer examination, however, reveals that structural plans express relations of far greater scope than do the morphotypes. The morphotypes of the head skeletons of the classes Mammalia, Aves, Reptilia and Amphibia are all different, but the structural plans expressed in these four morphotypes are essentially the same.

The following example is given to illustrate the construction of the morphotype as well as its meaning and limits. In the New World box turtle, *Terrapene*, the dermal bones that form the side wall of the skull either form a regular zygomatic arch continuous with the squamosal bone (*T. bauri*), or such an arch is entirely wanting (*T. ornata*). *T. carolina* and *T. triunguis* assume intermediate positions. Be it assumed that the morphotype of this skull region be constructed, based on the four species and involving, for the sake of simplicity, only the following bones: squamosal, quadrato-jugal, jugal and postorbital. In figure 3, the four bones are illustrated in horizontal series showing on the left side one extreme, on the right side the other extreme of their development in the four species under consideration. It is now necessary to determine which ends of these series hold the more generalized conditions. The question is readily answered by a comparison with the morphotype of the next higher systematic category, the family Emydidae. Here, the squamosal is in contact with the quadrato-jugal and the postorbital bone, dorsal to the tympanic funnel; the quadrato-jugal and the jugal widely contact the postorbital bone (fig. 6b). Thus, in figure 3, the condition of the bones at the left side of the illustration (1) is to be regarded as the generalized, 4 as the specialized end of the series. It is

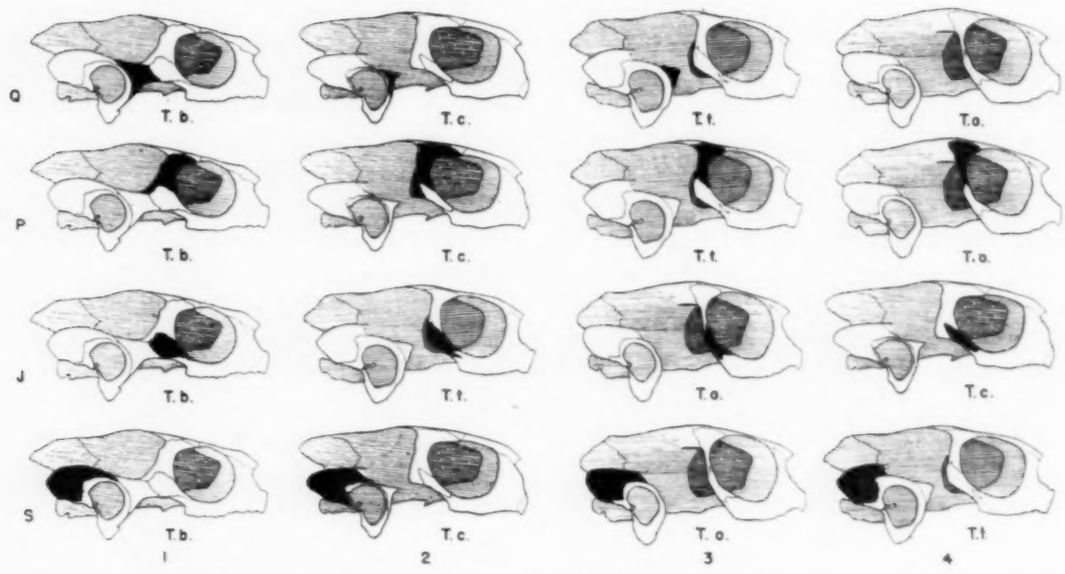

FIG. 3. Illustration to show four levels of differentiation of the four zygomatic arch elements in *Terrapene bauri* (Tb), *Terrapene carolina* (Tc), *Terrapene triunguis* (Tt) and *Terrapene ornata* (To). In each horizontal series, one bony element is shown in its range of expression within the four species. P, postorbital; Q, quadratojugal; J, jugal; S, squamosal. The vertical columns of figures (1–4) give the most generalized condition of the four bones on the left (1), the most specialized condition on the right (4). 2 and 3 represent intermediate conditions. Compare with figure 4 and text.

of no significance and due only to the choice of the species, that, in this particular case, all four generalized conditions are found in the same form, *T. bauri*. The morphotype of the bone pattern of the side of the skull, as derived from the conditions in the four species, includes the generalized conditions of the four bones under consideration. In this particular example, and only as far as the four bones are concerned, the morphotype is identical with the actually observed features in *T. bauri*. Figure 4 shows how the zygomatic arches of *T. carolina*, *T. triunguis* and *T. ornata* can be derived (ideally) from that of the morphotype by constructed intermediates.

This example was purposely chosen to show that the morphotype is a factual morphological tool, independent from phylogenetic speculation. The derivations in figure 4, involving contemporaneous forms, illustrate clearly that there can be no phylogenetic relations along the lines indicated. The same applies also to derivations in which the intermediates are actually documented by fossils, such as in the case of the derivation of the horse foot from the morphotype of the tetrapod limb.[6] The relations expressed in a series of derivative stages from a morphotype are never of a genetic nature. What is being expressed is rather a progressive series of relations of a particular kind, namely of homologies among different organisms. Its evolutionary significance is, however, in each case a problem by itself.

The widely held opinion that paleontology alone among the morphological sciences could claim to have a voice in the discussion of evolutionary problems, because of the "historic" nature of the materials, is a distinct fallacy. Its methodology is the same as that of comparative morphology in general, and the added factor of time, although an invaluable aid in the determination of the direction of a morphological specialization, is more than offset by the disadvantages of having but one structural system, the skeleton, available

[6] The difference in the two examples cited does not involve the methodological procedure, but the theoretical interpretation. With regard to the latter, the examples rest, of course, on entirely different levels.

for study. The following example is designed to show that in many cases comparative morphological results can, if properly achieved, be of such importance that even fossil documents can only confirm, but not further clarify or alter the results. For the sake of this demonstration, no mention will be made of fossils in the entire procedure, in spite of the fact that it is fossil evidence that gives us the strongest support for the argument.

The example, again, is selected with reference to the construction of the temporal and postorbital regions of the turtle skull. Figure 5 shows drawings of skulls in side view of 20 different species. All of these forms are Recent. A glance at the illustration shows that both the temporal and postorbital regions are greatly different in the selected species. In some forms, the temporal region is extensively roofed over; in others, it is more or less open. In some species, the ventral edge of the zygomatic arch is straight, but in others it is concave in varying degrees. Furthermore, the bones that cover the region differ greatly in their extent. The question presents itself as to the basic theme, the morphotype, from which all these varied conditions can be (ideally) derived.

1. The temporal region, although open in most turtles, is closed in some of them (*Dermochelys*, fig. 5A). A progressive series could be lined up to show the gradual, step by step, enlargement of the temporal fossa forward. In the extraordinarily specialized pleurodiran turtle, *Chelys fimbriata* (fig. 5-T), and other members of the family Chelydae, the posterior part of the temporal region is covered by a sheet of bone, the squamosal, connecting the quadrate with the parietal. Among other recent reptiles, e.g. the crocodiles, the temporal region is covered by bone

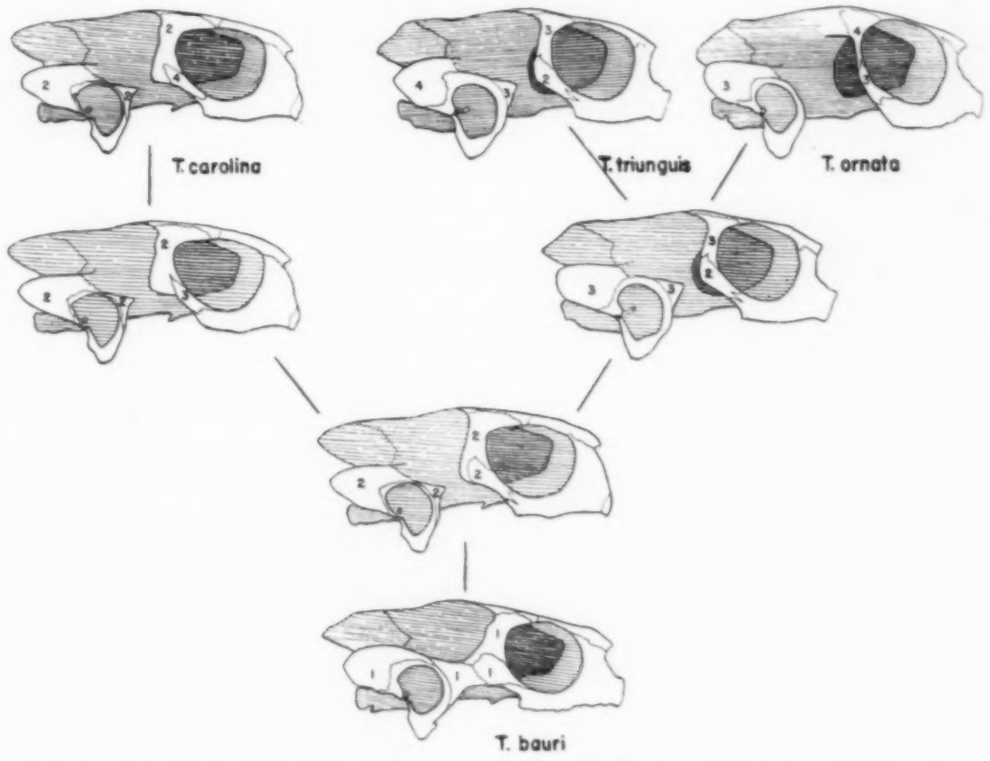

FIG. 4. Illustration of the morphotype concept based on analysis shown in figure 3. Bottom figure represents morphotype of the four bones considered among the four species compared. By coincidence, the morphotype condition is actually realized in *Terrapene bauri*. The actual conditions of the four bones in *T. carolina*, *T. triunguis* and *T. ornata* can be ideally derived from the morphotype by constructed intermediate conditions. For further explanation see text.

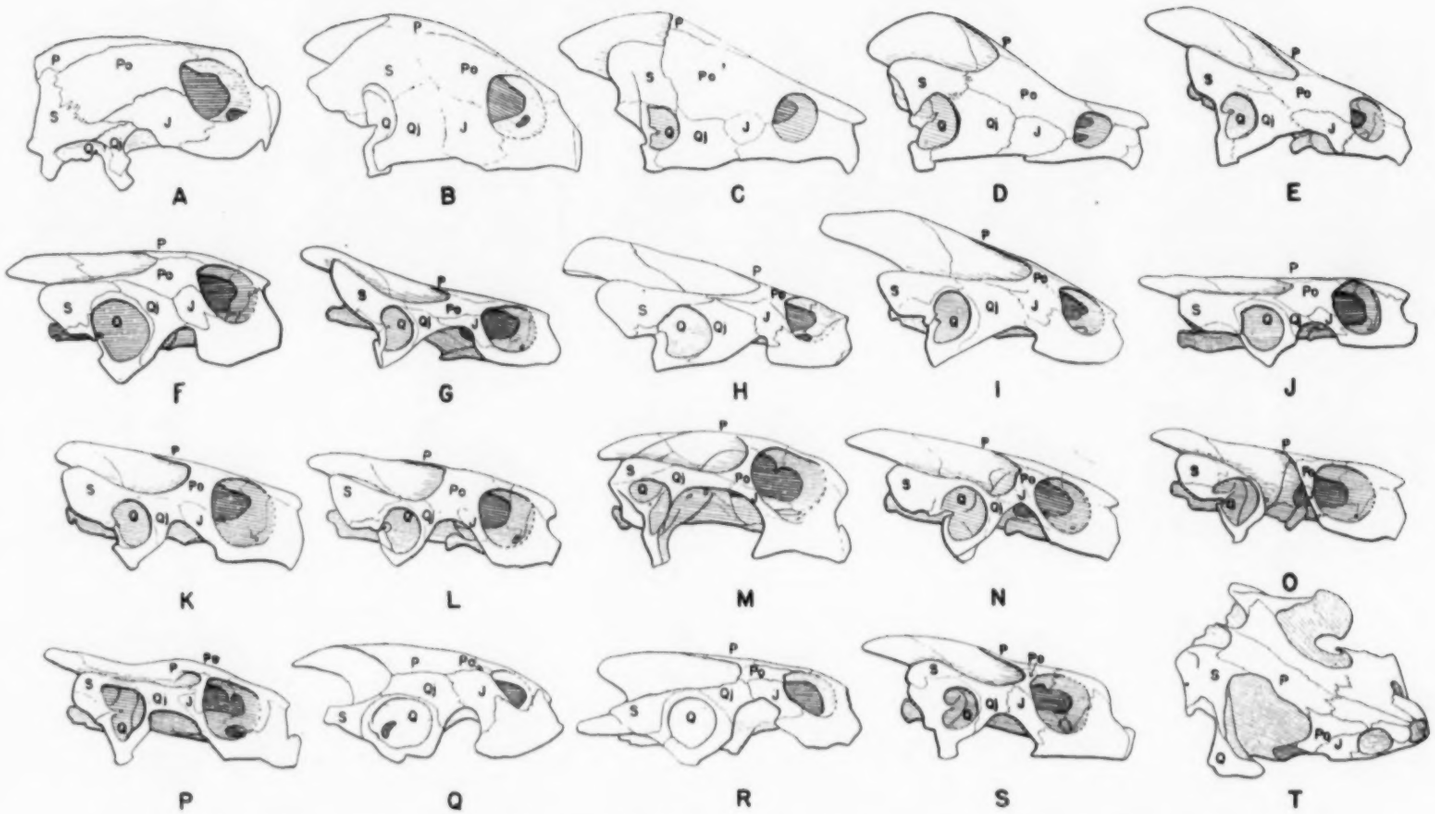

FIG. 5. Side views of the skulls of 20 species of recent turtles to show the postorbital and temporal regions.

P parietal
Po postorbital
S squamosal
J jugal
Qj quadratojugal
Q quadrate

A *Dermochelys coriacea* CNHM 58, B *Caretta caretta* CNHM 31021, C *Platysternon megacephalum* CNHM 6631, D *Macrochelys temmincki* CNHM 22111, E *Chelydra serpentina* Z 21, F *Pseudemys floridana* CNHM 22074, G *Emys blandingi* CNHM 31017, H *Graptemys geographica* CNHM 22177, I *Malaclemys pileata littoralis* CNHM 22124, J *Cuora amboinensis* CNHM 22173, K *Clemmys insculpta* Z 67, L *Clemmys caspica* CNHM 19714, M *Gopherus polyphemus* CNHM 31286, N *Nicoria triguga* CNHM 22054, O *Geoemyda spinosa* CNHM 22175, P *Kinixys belliana* CNHM 22082, Q *Podocnemis expansa* CNHM 16075, R *Pelusios sinuatus* CNHM 12699, S *Testudo pardalis* CNHM 22466, T *Chelys fimbriata* CNHM 22434.

except for two openings in the roof (diapsid condition). Posteriorly, it is closed by the parietal-squamosal-quadrate connection. This is also true in the rhynchocephalian *Sphenodon*. In the lizards, the large temporal opening is posteriorly bordered by a thin, bony rod that connects the quadrate with the parietal. In snakes and amphisbaenians, a temporal fossa in the ordinary sense is absent altogether, even though a posterior connection of the parietal with the quadrate by way of the squamosal is observed in some forms.

This review of the morphology of the temporal region in recent reptiles indicates that in all cases portions of a bony roof over this region are present, even at its aboral end. In view of the fact that the bony constituents in the region conform in all cases to a mutual structural plan, the varied conditions can only be formally derived from a morphotype of the order Reptilia in which the temporal region is completely covered, lacking fenestrae. Consequently, as far as this feature is concerned, the skull of *Dermochelys* (fig. 5-A) is generalized.

2. The ventral edge of the zygomatic arch in turtles is either straight as in *Caretta*, *Platysternon* and *Macrochelys* (fig. 5-B, C, & D), or it is more or less excavated as in *Chelydra* (fig. 5-E), *Gopherus* (fig. 5-M) and particularly *Chelys* (fig. 5-T). Much the same argument can be produced here as in the preceding discussion of the temporal roof. A straight zygomatic arch connecting the quadrate with the maxilla is present in crocodiles and in *Sphenodon*. In lizards, the arch is absent as in some turtles, *Geoemyda spinosa* (fig. 5-O), and in snakes and amphisbaenians, the entire region is so obviously modified as to be of no significance in the present discussion. Thus, a straight (unexcavated) zygomatic arch appears to be the generalized condition as exemplified in *Platysternon* (fig. 5-C).

3. The differences in the extent of, and the contacts between, the bones that make up the temporal and postorbital regions in the turtle species illustrated in figure 5 are largely due to the varying sizes of the temporal openings and zygomatic excavations. But there are at least two diametrically opposite conditions in the size relationship of the parietal and the postorbital bones. In *Dermochelys* (fig. 5-A) and in the great majority of the species where judgement is possible (in forms with large temporal excavations it is difficult to tell), the postorbital bone is large, whereas the parietal is of moderate size. In *Podocnemis* (fig. 5-Q), on the contrary, it is the parietal that is by far the largest bone of the region. The postorbital is tiny, occasionally even absent (Ruckes, 1937). The latter condition is rare among turtles, so that it appears safe to consider the former the more generalized character.

Thus, the morphotype of the temporal-postorbital region of the turtle skull lacks both dorsal and ventral excavations. The squamosal makes sutural contact with the parietal, postorbital and quadrato-jugal (fig. 6-A). From this morphotype, the three following, essential conditions represented by the selected species in figure 5 can be ideally derived:

1. (fig. 6-B) Postorbital bone relatively large, parietal moderate in size; contact between squamosal and parietal broken by dorsal excavation, or rarely present, where excavation is small. Ventral excavation (usually smaller than dorsal) tending to disrupt contact between jugal and quadrato-jugal. Occasionally dorsal and ventral excavations merge into one (*Geoemyda spinosa* (fig. 5-O).

2. (fig. 6-C) Parietal is enlarged, postorbital reduced in size, sometimes even absent. Dorsal and ventral excavations moderately large (*Podocnemis*, fig. 5-Q).

3. (fig. 6-D) Dorsal excavation small, ventral excavation enormous; connection between squamosal and parietal retained (*Chelys*, fig. 5-T).

The morphological results here obtained without the benefit of fossil evidence must readily be admitted in the face of the fact that one of the oldest and best known turtles (*Triassochelys dux*) agrees in every

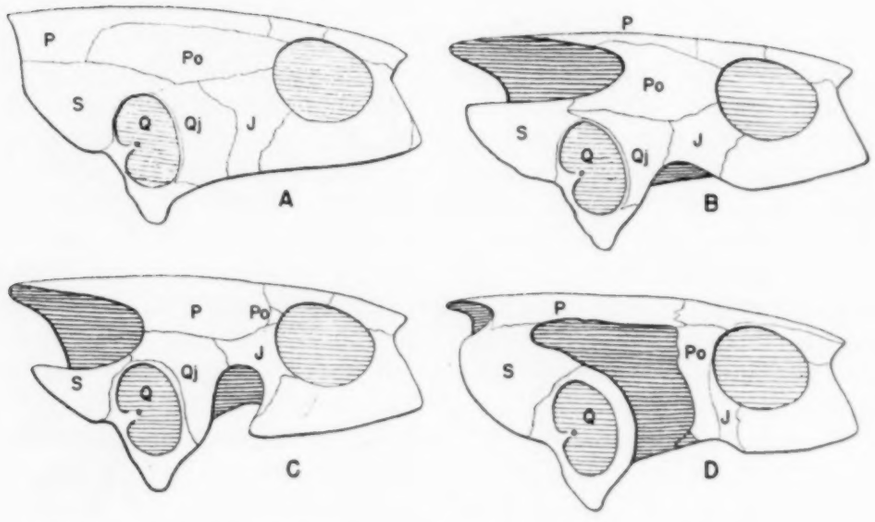

FIG. 6. Illustration of the morphotype (A) of the postorbital regions of the turtle species in figure 5. B, C, D represent the three essential conditions of this region of the skull in the species of figure 5. B, C, and D can be ideally derived from A (see text for further explanation).

essential respect with our constructed morphotype. The presence of separate postfrontal and postorbital bones as well as a supratemporal in the skull of *Triassochelys,* for which bones there is no evidence among recent forms, does in no way invalidate our results. Neither will suggestions by possible skeptics that the writer had the condition of *Triassochelys* in mind when constructing the morphotype, because, even if this were true, the argument nevertheless was carried without reference to fossil conditions and is thus valid and applicable in structural systems where fossil evidence is completely lacking (soft anatomy).

The concept of homology

Few concepts in biology have had as turbulant a history as that of homology, and its discussion, particularly in the most recent English language literature has almost entirely overlooked the methodological nature of the *concept* and dealt primarily with the causality of the *phenomenon* (except Boyden, 1947). A few citations may serve to illustrate the situation. Hyman (1943), p. 3: "This question (of the relation of form and function) involves the concepts of homology and analogy, which are understandable only in terms of the principle of evolution. Homology is intrinsic similarity indicative of a common evolutionary origin." Hubbs (1944), p. 290: "Homology has thus come to signify agreement in evolutionary derivation" and "Proof of homology has become the basis of phylogeny," and p. 292: "It is high time that we think and write of homologous functions in the same way that homologous structures have been treated, and that we discard from the definition of homology any necessary restriction to anatomy." Boyden (1943), p. 240: "Homology is a genetic phenomenon and both serial and special homology are based upon mechanisms which involve the interaction of genes and cytoplasm . . . "and" . . . special homology bears directly upon the analysis of racial descent." Haas and Simpson (1946), p. 324: "Homology as here understood is still a well usable phylogenetic term" and p. 344: "Owen's (special) homology should be restricted to similarities between parts, organs or structures of different organisms attributable to common ancestry"; and Simpson (in Haas and Simpson), p. 323: "In such cases, I can see no objection to speaking of homologous functions, as

an expression of opinion as to the origin of a dynamic complex including the functions along with the structures performing them"; and p. 325: "Homology, as we agree, is best defined as similarity interpreted as due to common ancestry. Homoplasy, as we also agree, is best defined as similarity (or as including *any* process leading to similarity) that is not explicitly interpreted as due to common ancestry. Both terms, rather than being purely descriptive (as in Boyden's definition of homology, for instance), express an opinion, one positive and one negative."

While a discussion of the possible causality of a phenomenon such as a homology is perfectly legitimate, the authors cited failed to realize that this is not the case with the concept as such. This failure brought about a great many difficulties that render the concept practically worthless (see Hubbs, 1944 and Etkin and Livingston, 1947).

A great deal of the confusion is due to the phylogenetic implication that has been injected into the concept. It was repeatedly pointed out that such procedure involves a *circulus vitiosus* (Kälin, 1941, p. 6): the criterion of homology of organs or parts is said to be common phyletic origin of these structures, whereby the supposed common origin itself is to be established by the very demonstration of their homology! Recent efforts to analyze the causal factors that bring about a homology are obviously fruitless endeavors, since it is all too well known that structural plan similarities, i.e. homologous features, can either have arisen from a common origin, or, independently, in different lines. Thus, an individual homology between two or more organisms is indicative of neither of these possibilities, but merely postulates a particular relation between the compared parts, a relation that we call a homology. If we define the concept as Haas and Simpson (1946) do: "Homology, as we agree, is best defined as similarity interpreted as due to common ancestry," we rob the concept of its only possible function, namely as a tool, since we do not and cannot, *a priori*, know anything about the causality of a given structural relationship between parts of different organisms.

A second difficulty is the repeated attempt by various authors to broaden the concept of homology to include similarities other than those presented by structural correspondance in organisms, such as, for instance, similarities in function and in behavior patterns; to cite only one instance (Hubbs, 1944, p. 292): "The clawing of a cat and of a tiger has much the same meaning as does the homology of the claws." We have already intimated that homology expresses a particular kind of structural relationship, intimately interwoven with such more inclusive concepts as those of the structural plan and the morphotype. These, however, cannot be applied to functions and behavior patterns in the same way as to structures. If, in the analysis of functions and behavior patterns, a special terminology to cover the concepts should be necessary, then such a terminology should be adopted (a beginning has already been made by Abel, 1912, and Böker, 1935). Borrowing a concept from one discipline and applying it in another, where it is outside the realm of its applicability, is definitely suspect. This has been clearly demonstrated in Spemann's (1915) critique of the homology concept. Colucci (1891) and Wolff (1894–5) showed in elegant experiments that the lens of the eye, after operative removal, will regenerate from the mesodermal tissue. Kälin (1935) points out correctly that the total breakdown of the homology concept in the field of developmental mechanics does in no way invalidate it in morphology, since the lens, *normally*, always develops from the ectoderm.

A third source of confusion lies in the lack of clarity as to the intra- and inter-individual form relationships. The argument involves the question of greater or lesser degrees of structural correspondence among serially arranged organs *within* the individual or between homologous organs

among individuals. Boyden, 1943, comes to the conclusion that there is a greater degree of correspondence among homologous organs than among serially arranged, intraindividual ones and cites as evidence a comparison of the appendages of two crustaceans, *Homarus* and *Callinectes*. Hubbs (1944), in answer to Boyden, suggests another example, also chosen from among appendages of crustaceans (pereiopods 2 and 3 of the lobster and blue crab), that presents the exact opposite situation. Hubbs feels that intraindividual form-relationships are of no less importance in their "evolutionary significance" than are such relations among different organisms. He continues (op. cit., p. 293): "Broadening comparisons, we often find vastly greater correspondence in anatomy, and in homology, between serial structures in one individual than between the 'same' structures in two animals. Thus, we see vastly greater agreement in fundamental structure and relationships of parts when we compare the fore limb and the hind limb of a horse, than we do when we contrast the fore limb of a horse with its special homolog, the pectoral fin and girdle of a teleost fish." Thus, Hubbs suggests the abandonment of a distinction between intra- and interindividual form relations and illustrates his point by reference to structures that are dispersed at random, or that are units of a pattern, e.g. scales, feathers, hair, etc.

An analysis of the examples cited in this dispute readily reveals the source of error. First of all, as has been pointed out by a variety of authors (Kälin, 1941; Böker, 1935, Uexküll, 1928; and others), and as has been demonstrated in an unusually impressive manner by the phenomena of development in experimental zoology, the ultimate nature of an organism lies in its *entirety*. It is not, in other words, a conglomerate of more or less independent parts, functions and behavior patterns in a given environment. This fundamental realization has produced profound effects in all aspects of biological research and could not fail to achieve, in morphology, a refreshing clarification of its methodological concepts. Comparison of the structural similarities between the fore and hind limbs of a horse with regard to the individual as an organismic entity expresses, obviously, an entirely different relation than comparison of the fore limbs of two or more horses. Thus, a distinction between intra- and interindividual form relations must be upheld.

Kälin (1935, p. 658) defines intraindividual form relations as follows: "Parts, so arranged with regard to the whole of one and the same organism that they correspond with each other in certain geometric aspects, are best called intraindividually plan-similar, or homonomous." He continues to explain: "Homonomy includes those relations in the fundamental geometric pattern as are represented by bilateral symmetry, metamery and paramery, i.e. those relations of parts within one and the same individual that are known as homotypy (antimer-homonomous) and homodynamy (metamer-homonomous and paramer-homonomous)."

It may be noted that there are different relations between multiple intraindividual structures, agreement to the basic geometric arrangement of the body being only one of them. Foremost among these are agreement in histological and cytological differentiation (hairs, sweat glands, cilia, spines of sea urchins, etc.) as well as in specific shape (scales, hairs, feathers, etc.). Multiple organs have caused considerable discussion with regard to their homology (see below).

The interindividual form relations present a somewhat more complicated picture. Homology is one of these relations, but, although the most important one, it is by no means the only one. In the correspondence of structural elements of two or more organisms according to a common structural plan, Kälin (1935, 1941) distinguishes as the most important categories of plan-conformity in comparative anatomy:[7]

[7] Kälin calls these "planmässige Kategorien der vergleichenden Anatomie."

1. *Homology*, the fundamental category (discussed below).
2. *The category of the special topographical relationships.*
   Correspondence of homologous parts in the special topographic relationship to other parts; e.g. correspondence in the subterminal position of the mouth opening in selachians; correspondence in the precaudal position of the anus in vertebrates; correspondence in the position to each other of the middle ear ossicles in the cavum tympani of mammals.
3. *The category of the histological differentiation.*
   Correspondence in the histological differentiation of homologous parts (it is of importance in the skeleton, depending on whether homologous parts ossify secondarily, remain cartilaginous or occur as membrane bones), e.g. the vertebral columns of different mammals but not those of mammals and Chondrichthyes.
4. *The category of the cytological differentiation.*
   Correspondence in the cytological differentiation of homologous parts; e.g. differentiation of the melanophores among different amphibians; certain cells of homologous regions of the cortex of the brain.
5. *The category of the specific shape.*
   It lies in the correspondence of homologous parts with regard to their particular shapes; e.g. hypselodonty of incisors in mammals; also the particular relief of the molars, according to which they are called bunodont, selenodont, secondont, lophodont, etc.; kidneys in dog and man.
6. *The category of the number.*
   Correspondence in the numerical occurrence of certain homologous parts; e.g. 7 cervical vertebrae in mammals; 5 premaxillary teeth in crocodiles, etc.
7. *The category of the promorphological relationships.*
   Correspondence of homologous parts with regard to the basic geometric patterns of the organisms. Into this category belong particularly correspondences of homologous parts which, at the same time, stand in an intraindividual relation to each other, namely that of homonomy (homotypy, homodynamy and paramery) on the basis of bilateral symmetry, metamery and radial symmetry (homonomous homologs).

To these we may add:

8. *The category of the isodynamic planstructure.*
   It consists of the correspondence of homologous parts with regard to their functions, e.g. claws of cat and tiger, etc.

This analysis shows clearly that there are various kinds of correspondences among parts of different organisms. The compared structures may be homologous, but, in addition, another relationship may be correlated with the homology, such as comparable histological differentiation, particular shape, etc. Homology is only one, but the most fundamental interindividual form relation between members of a common morphotype.

It is not, in this place, necessary to enter upon a discussion of the history of the homology concept, this having been done exhaustively elsewhere. In its original definition, Owen (1846) stated that "The corresponding parts in different animals . . . being homologues." This definition, although essentially correct and still acceptable now, may easily lead to misinterpretation, as it undoubtedly did in the past, because it does not specify what is to be understood by "corresponding parts"; e.g. the quadrate and articular bones in Sauropsida on the one hand and

the squamosal and dental bones in mammals on the other correspond with regard to their position at the apex of the jaw angle, but the two sets of bones are not homologous. As a methodologic tool, a concept such as that of homology needs to be sharpened in accordance with the progress made in its field, but not, as has almost universally been done, by its transfer into the theoretical discussion. It must here be stated that it is to the credit of Naef, Jakobshagen and Kälin that they further evolved the concept within the realm of its applicability, and Kälin, in particular, has furnished a clear and modern definition which in itself well demonstrates the advances made in morphology since the days of Owen.

Kälin's definition (1945): "Homology exists, if parts of different organisms correspond to each other within the common structural plan and morphotype of a given systematic category." [8]

Here, then, is a definition that does justice to the holistic nature of the organism. Homology is structural correspondence with regard to the organism as a whole, not just this or that other part of it; it is correspondence with reference to the common structural plan and morphotype of the compared organisms.

In this formulation and with its present content and relationship to the morphotype, the homology concept has become uniformly applicable to all the diverse material that has been subjected to morphological study. But a few additional explanations seem in order.

1. It is a fairly common experience to find cases in which structural elements are differentiated that are not realized in the morphotype to which the form in question belongs. For instance, in several genera of trionychid turtles (*Lissemys, Cyclanorbis, Cycloderma*), there is a bony plate in front of the bony carapace (prenuchal bone) which is not present in any other recent trionychid, and which is not part of the morphotype of the family Trionychidae. This and similar examples show that homologous structures are either fully expressed in the morphotype or the group to which the compared forms belong, or they may be represented in the morphotype only by an undifferentiated region. Kälin proposes to call homologues that are structurally represented in the morphotype *typophaenous* homologues, those represented in the morphotype merely by an undifferentiated region *atypophaenous* homologues.[9]

2. Occasionally, the opinion is voiced in the literature that there are various degrees of homology. Jakobshagen (1924), for instance, distinguishes a highest degree of "complete" homology which he calls "Orthomologie" from lower degrees called "Kathomologie." Kälin (1941) pointed out correctly that such an attempt was based on the erroneous assumption that homology as a basic category of plan-comformity could itself have different degrees. Gegenbaur (1870) distinguished in his "special homology" a "complete" and an "incomplete" (partial) homology. Naef (1926) contends that such a distinction is superfluous because a partial or incomplete homology does not exist. Kälin (1941), granting Naef's contention as essentially correct, nevertheless suggests that we retain Gegenbaur's terminology, arguing that the attributes "complete" and "incomplete" need not be taken literally as qualifying the status of homology, but merely express, quantitatively, the extent to which structures conform in compared organisms. An example will illustrate the situation in question. The morphotype of the plastron of the pelomedusid turtles contains a pair of mesoplastral plates that separate the hyoplastra from the hypoplastra. They extend from the longitudinal midline of the plastron to the marginal bones. One of the living representatives

[8] Kälin (1945, p. 13): "Homologie besteht darin, dass Formteile verschiedener Organismen im gemeinsamen Typus-Bauplan einer bestimmten systematischen Kategorie sich entsprechen."

[9] Naef suggested the terms "typical" and "atypical." Kälin modified this terminology on the ground that "atypical" homologues also can be related to the morphotype.

of the family, *Pelusios,* has a plastron essentially identical in regard to the mesoplastron as the morphotype of the family. In the other recent representatives of the family Pelomedusidae (*Podocnemis, Pelomedusa*), mesoplastra are also present, but they are relatively small, more or less circular plates, laterally wedged between hyo- and hypoplastra and the marginal bones. There is an incomplete or partial homology of the *Podocnemis* mesoplastron and that of *Pelusios,* because, with reference to the morphotype, the former is completely homologous only with the lateral extent of the latter (fig. 7).

An excellent diagram to illustrate the homology concept was given by Kälin (1935, 1941). This is here reproduced with minor modifications (fig. 8).

3. It is a well-known observation that individual units of the structural plan sometimes undergo profound changes during ontogeny. These changes often involve considerable displacement of structures from one part of the body to another. To quote an example from Hubbs (1944), p. 298: "Thus, the membrane bones (in fishes) shift from the exoskeleton to the endoskeleton, to become covered by unmodified scales; when accessory scales are developed, the homologs [10] come to lie three deep." This and many other onto-

[10] According to our concepts, these structures are not homologues.

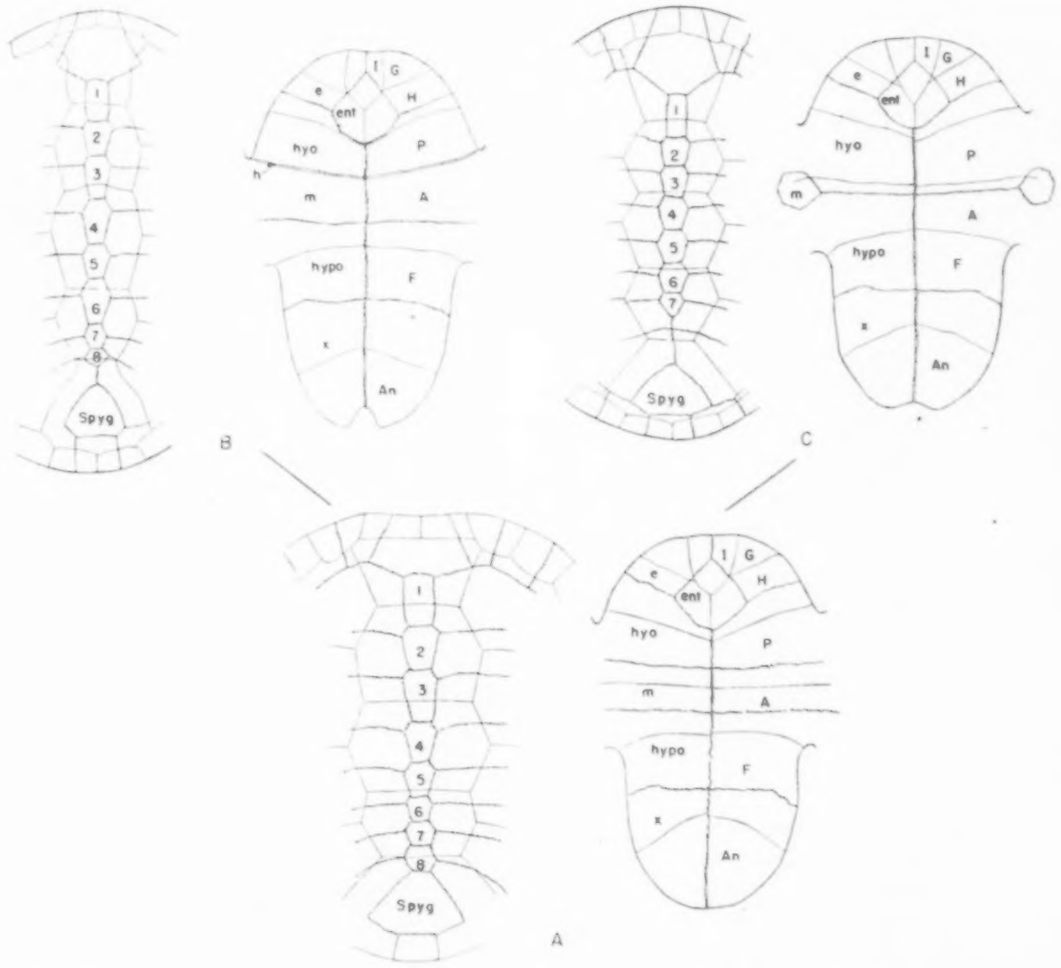

FIG. 7. A, the morphotype pattern of the pelomedusid shell; B, the pelusiine morphotype pattern; C, the pelomedusine morphotype pattern. With regard to the morphotype A, the mesoplastron (m) in C is partially homologous to the mesoplastron in B. From Zangerl, 1948.

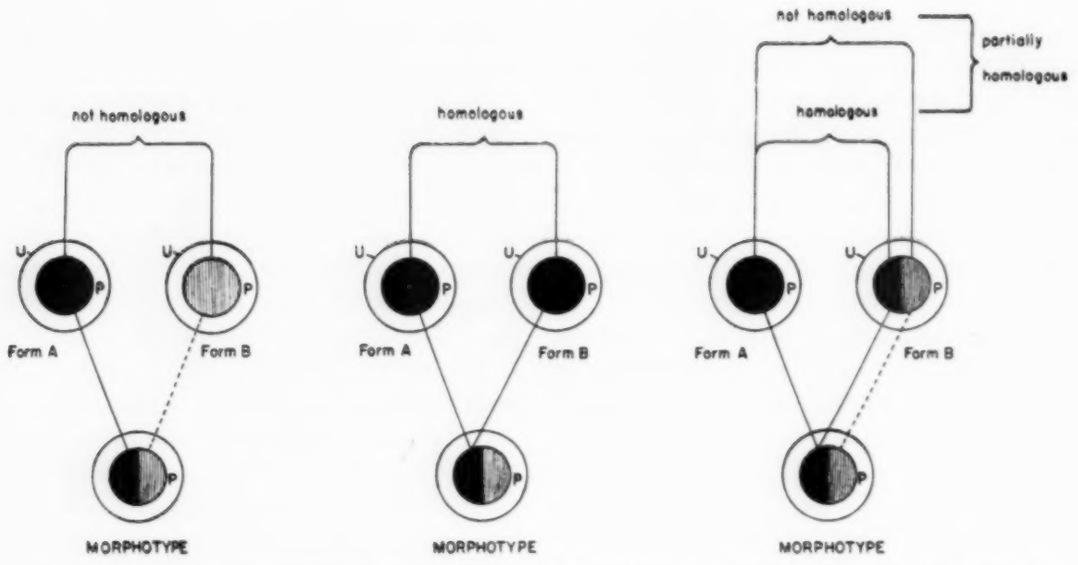

FIG. 8. Scheme to illustrate the concept of homology. Each circle (U) indicates the mutuality of the structural plan and morphotype in the compared organisms (Form A and Form B). The compared parts (P) are represented in black or in shading. Insofar as they are homologous with regard to the morphotype, they are represented in black. (From Kälin, 1935 and 1941, redrawn with minor modification.)

genetic examples of this general sort need careful analysis with the sharpest of methodological procedure, if utter confusion is to be avoided (see Kälin, 1945, concerning Peter, 1922 and 1938). It is in problems of an ontogenetic nature that the four dimensional concept of the morphotype merits particular distinction. It has served to a great extent to clarify von Baer's principle,[11] as well as to remove the controversy surrounding it, centering on "caenogenesis" (see also Kryzanowsky). It led, furthermore, to the formulation of Kälin's principle of formative irreversibility in ontogeny, which states that ontogenetic form-differentiation is insofar irreversible as the material (of structurally lower morphotype value, thus of greater complexity) that has developed from a material unit of higher morphotype value (thus of lesser complexity) cannot return in its entirety to the condition of a higher morphotype by reversal of the formative processes. This statement is of basic importance to the use of the homology concept in ontogenetic problems. It is the basis for the conclusion (statement of the ontogenetic precedence of homology by Kälin, 1936 and 1945; see also Naef, 1919) that parts "that have been recognized as homologous at a given stage of development, with regard to a particular morphotype, remain, with regard to the latter, homologous throughout all subsequent transformations."

4. The homology of multiple structures, such as vertebrae, myomeres, teeth, hairs, scales, etc., has presented problems that induced rather heated controversies in the literature. The confusion of intra- and interindividual plan-similarity accounts for some of the difficulties (see p. 364); but there still remains the question as to what parts of multiple structures are to be considered homologous, e.g. in two closely related organisms in which these structures appear in different numbers (cervical vertebrae in different birds, scales in fishes, etc.). The problem is further com-

[11] Von Baer's principle of individual development states that those features of a larger group of animals that are mutually present among them develop earlier in the embryo than the particular characters of the individuals. This sentence is the expression of the fact that ontogenetic development proceeds, *cum grano salis*, from the general to the special, i.e. from higher (more inclusive) to lower (less inclusive) morphotype characters (Kälin, 1945).

plicated by the fact that in some organisms individual elements or groups of multiple structures become particularly differentiated, or stable numerically (certain dorsal scales in teleost fishes, scales related to the organs of the lateral line; cervical vertebrae in mammals, etc.).

Here, as elsewhere, only a homology concept that is closely related to that of the morphotype can produce clarity. A few examples will illustrate this point. The body of a teleostean fish is covered by large numbers of unmodified scales, whose number varies greatly from genus to genus and even from one species to the next. Consequently, the number of unmodified scales in the morphotype of the teleost fishes is not stable, from which follows that every unmodified scale in one form is homologous to all the unmodified scales in all other teleost fishes; this applies in all those cases where undifferentiated multiple structures occur in different numbers among the compared forms and in whose mutual morphotype this number is unstable.

Very often, however, some multiple structures or groups of them are differentiated in a particular way. So, e.g., individual scales in some groups of teleost fishes are enlarged and assume a particular shape (preanal, caducous scales in some perches, *Percina*). In such cases, the differentiation is a part of the morphotype of the group, in the example mentioned the genus *Percina*, and therefore the question of homology presents no problem, at least none with regard to the whole series of these scales. If, in *Percina*, the number of scales in this series differs from species to species, then each of these modified scales in one species is homologous to all scales of the row in the next species; if, however, the number should be the same in all representatives of the genus, then the number would also be part of the morphotype of the genus *Percina* and consequently each scale in one species would be the homologue of the numerically corresponding scale in the other species.

Differentiation of multiple structures within the morphotype of a group has been called homologic specialization. The modification of the vertebral column into regions (cervical, thoracic, lumbar, sacral, caudal) represents an illustrative case of homologic specialization. Within the morphotype Tetrapoda, for instance, the neck region of the vertebral column is homologous throughout the members of the group, regardless of the number of vertebrae that it may include (2 in the frog, 76 in *Elasmosaurus*); in the mammals (other than tree sloths), another homologic specialization stabilizes the number of cervical vertebrae to 7. Within the morphotype Mammalia, therefore, each cervical vertebra in one mammal is homologous only with the numerically equivalent element in other mammals.

The value and applicability of the homology concept as here defined can hardly be overestimated, in view of the fact that, for instance, Hubb's "ineradicable complexities" vanish into non-existance by simple test of the various examples cited by that author.

Little need be said about the concept of analogy. If two or more parts of organisms, within their common structural plan and morphotype, correspond with each other in regard to their function *only*, they are analogues (e.g. gills and lungs within the morphotype Vertebrata, etc.).

The morphological series

Morphological series are among the most efficient techniques to demonstrate anatomical relations of all kinds, but, at the same time they are a constant source of misunderstanding, if their erkenntnistheoretic quality is not clearly understood. It was pointed out above (p. 353) that the materials subject to morphological study are of a very different nature; this recognition must be kept in mind constantly when morphological series are to be properly evaluated. It was further noted above (p. 364) that parts of an organism can be properly understood only in their relation to the organism as a whole; in other words, the basic nature of

morphology is holistic. Since almost all of the morphological series are concerned with only parts of the organisms compared, this consideration is of the utmost importance in the interpretation of all such series.

Morphological series are essentially series of homologues and as such they must always be considered with regard to the common morphotype and structural plan of the organisms compared; the scope of the morphotype (its greater or lesser inclusiveness) determines, in direct proportion, the interpretative value of the series; the higher (less inclusive) the common morphotype of the representatives of the series, the less its overall significance, and vice versa.

If a morphological series includes adult as well as embryonic form-stages, the four-dimensional nature of the morphotype must be carefully considered, which adds to the difficulty of a proper morphological interpretation of the series. If form-stages of fossils are added to the series, its morphological evaluation requires the very greatest of care.

It will be noted that I have consistently spoken of "morphological interpretation." This is because all too often premature attempts at phylogenetic evaluation or morphologically uninterpreted conditions are made. The morphological (factual) interpretation, which must always precede the phylogenetic evaluation in correct methodology, is left out. Needless to say, such procedure harbors many dangers and should be avoided in the interest of sound theoretical argument; but aside from this, it robs morphology of its own results, which, as will be shown under the heading "empiric principles," are important factors in the further investigation of the "form problem."

Empiric principles

The study of the organismic form problem reveals a very great number of *gesetzmässigkeiten* [12] in the form differentiation. Of the vast multiplicity of ideally conceivable form expression, only a relatively small segment is actually realized. It is the ultimate task of morphology as an empirical science to uncover these *gesetzmässigkeiten* within the actually realized segment of form expression and this is usually done in the form of empiric principles. The erkenntnistheoretic value of empiric principles in morphology is as varied as that of morphological series, some have wide applicability, others do not. Among the former, von Baer's principle of ontogenetic development and Kälin's principle of irreversibility in ontogeny as well as Dollo's principle of irreversibility in evolution may be mentioned. Among the latter, a great many examples could be cited, but most of them have not been formally stated. For instance, aquatic adaptation in turtles is expressed in very definite patterns that seem to recur in unrelated groups. An empiric principle with a somewhat wider scope is Williston's law as formulated by Gregory (1935), which says that the number of skull bones decreases from the lower to the higher vertebrates.

It may be pointed out that many of the empiric principles have suffered undue criticism at the hands of biologists who failed to understand their true nature. The controversy regarding Dollo's principle of irreversibility of evolution may serve as a pertinent example. Basically, any such principle is factual and thus it cannot be invalidated as such; its range of applicability may, however, prove to be much more restricted than first assumed, so that its over-all importance may suffer. Furthermore, these principles are based on morphological evidence and their significance is thus restricted to the realm of morphology. They cannot be "tested" by the results of other biological disciplines.

As already intimated above, empiric principles may provide important insight into the form problem, particularly its

[12] The German word is here introduced for lack of an English equivalent. It means essentially conformity to various kinds of basic patterns in nature.

historic, paleontological aspects. An example may serve to make this clear. Rütimeyer (1867 and 1873), in his classical monograph on the late Jurassic turtles of Solothurn, classified these forms among the recent families Emydidae (Cryptodira) and Chelydae (Pleurodira). This was done with entirely proper morphological methods, but at a time when sufficient insight into the *gesetzmässigkeiten* of the organization of the turtle body was not yet available. Consequently, Rütimeyer classified the Solothurn forms according to the available criterion, namely, the greatest degree of over-all structural similarity. Today, empiric principles concerning turtle morphology are at hand and they permit the demonstration that greatest similarity is often an unreliable criterion for determining morphological relationships, particularly in geologic-historical material. It is here that empiric principles are of the greatest importance, since they may point out morphological relationships among rather dissimilar forms, whose structural organization, however, indicates certain trends of differentiation established elsewhere. In groups where empiric principles are still wanting, adequate establishment of morphological relationships is very difficult and largely unsatisfactory. Thus, Welles' discussion of the relationships of the plesiosaurs to other groups of reptiles (1943) can only be regarded as provisional largely due to lack of such knowledge.

The Meaning and Limits of Morphological Results

Before sketching the role that morphology plays in the general discussion of evolution, it may be of some value to consider briefly the nature of morphological results as obtained by the methods outlined above. Morphology, like all other sciences, has its own domain of theoretical evaluation of its results. In this case, we speak of morphological theories, in contrast, for instance, to phylogenetic (evolutionary) theories. This distinction must be upheld, because the two kinds of theories do not rest upon the same erkenntnistheoretic plane, and are not, therefore, identical. The morphological theory explains how one structural complex can be derived, ideally, from another, but it does not claim that one represents the ancestral condition to the other in the sense of blood relationship. A good example in point is Reichert's theory demonstrating the origin of the mammalian middle ear ossicles in elements of part of the masticatory apparatus of primitive vertebrates. The theory does not say that the mammalian stapes has actually developed from a reptilian stapes and the latter from an elasmobranch hyomandibular cartilage. It merely states that within the morphotype Vertebrate, the elements cited exhibit a particular morphological relationship and that the three conditions can be ideally derived from one another in the well-known manner. Thus, here, as in its methods, morphology remains free from phylogenetic hypotheses. The value and significance of morphological theories depend on the nature of the materials upon which the theory is based and on the quality of the underlying analysis. This becomes particularly clear when the morphological theories are considered which attempt to explain the origin of the Craniota, and, in contrast, those concerned with the derivation of the recent horses.

The Contribution of Morphology to the Discussion of Evolution

As pointed out in the introduction, Naef and Kälin have been accused of "advocating a return to pre-evolutionary thinking." This is a misrepresentation of fact. Their work, as well as the present article, merely attempts to separate phylogenetic thinking from morphological thinking, and to put both on a sounder basis.

It is a well known fact that morphological results of all kinds can be translated into phylogenetic, i.e. evolutionary terms. Such procedure is logically sound and desirable, provided the nature of phylogenet-

ically interpreted, morphological conclusions is clearly understood by everybody concerned. It must, first of all, be remembered that a given morphological interpretation may be sound, while its phylogenetic translation may not be; this is perfectly obvious in cases such as those mentioned by Hubbs (1944) cited above (p. 354). For this reason, it can hardly be overemphasized that the morphological interpretation (with careful consideration of its meaning and limits) must always precede a phylogenetic conclusion, so that the speculative elements, hereby introduced, can easily be recognized.

It has recently become the practice of some biologists working on morphological problems not only to interpret their findings in the light of present day evolutionary theory, but to use concepts of other biological disciplines (primarily of genetics) in their methodological approach. This practice produces results that readily agree with recent theoretical thinking, which is to be expected *a priori*, since the theoretical concepts themselves are used as the method for achieving the results. It seems that many scientists, in the enthusiasm over new achievements, are prone to fall victim to fallacies of this sort. This new variety of scientific self-deception is essentially not different from that engaged in during the latter half of the last century, when the "biogenetic law" was regarded as the key to many, if not all, phylogenetic questions, and was used indiscriminately as a working method (as distinguished from a working hypothesis).

There is yet another reason why concepts of other biological disciplines cannot be used in the study of morphological problems. This has been pointed out by several authors in the past and requires emphatic restatement here. None of the concepts developed in the field of genetics to this date is of a holistic nature. These concepts are based on usually minor aspects of the structural organization of the organism, so-called "characters" or, and this is a step forward, on field control by individual genes or gene groups. But an organism neither consists of independent individual characters nor of groups of such; its very nature lies in its entirety. It was demonstrated in this article that this recognition permeates all of the morphological concepts, whereas in genetics, comparable concepts do not exist and, indeed, may not be necessary or desirable. In the interest of sound further development of our understanding of the over-all problem of evolution, it is necessary to keep in mind that it is a working hypothesis to assume that genetic concepts of the nature available at present can be applied without reservation to complicated structural mechanisms, and even entire organisms.

It is in this basic realm where morphology must and can make an important contribution to the future development of ultimate theoretical thinking in biology.

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Summary

The present essay contains a restatement of comparative morphological methodology, with particular emphasis on the content and meaning of its concepts. It further indicates the particular contribution that morphology can make to the overall discussion of problems related to evolution.

1. Morphology, like experimental sciences, has its own method. In experimental fields, it is the experiment; in morphology, it is observation and comparison. The concepts derived

from these are usually called the morphological method.

2. The concepts of the morphological method are factual, since they express various relationships whose reality lies beyond the activity of the human mind.
3. The most important concepts of the morphological method are the structural plan, the morphotype, homology, the morphological series and empiric principles.
4. The concepts of the morphotype and the structural plan are closely related. The morphotype is the ideally constructed form, the norm, within a group of organisms of essentially similar structural design, from which the actual forms of that group can be ideally derived. The structural plan expresses the conformity in the topographic relationships of the parts to the whole of the morphotype.
5. The concept of homology is holistic in nature and directly related to those of the morphotype-structural plan. Kälin's definition states: "Homology exists, if parts of different organisms correspond to each other within the common structural plan-morphotype of a given systematic category."
6. "Phylogenetic" homology definitions involve a *circulus vitiosus* and must be discarded. Function cannot be considered as a criterium in homology.
7. All concepts of the morphological method are holistic in nature, i.e. they are related to the organism as a whole. Morphology, by the very nature of this approach, can benefit the future development of theoretic thinking in biology.

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NOTES AND COMMENTS

CLIMATIC RACES IN PLANTS AND ANIMALS

Differences in habitus between local populations of plants have been known to naturalists for a long time. That some of these differences had a genetic basis was obvious from early transplantation experiments, but it was Turesson (1922) who initiated systematic experimentation in this field. These studies have been continued by Gregor and other workers, but have reached a climax in the work of the Stanford group of the Carnegie Institution (Clausen, Keck, and Hiesey). In their latest publication [1] these authors have studied various populations of yarrow (*Achillea*). The members of *Achillea millefolium* complex almost blanket the temperate and subarctic regions of the Northern Hemisphere. Furthermore, they are not only geographically but also ecologically widespread. In central California, for example, they occur almost without interruption in all the major environments from the salt spray drenched shore of the Pacific through the torrid San Joaquin valley to the alpine zone of the Sierra above timberline and down again to the edge of the Central Basin. Plants from eighty localities were studied and grown in experimental gardens under uniform conditions. These populations have two outstanding characteristics. One is the pronounced variability within each population, and the second that in spite of this variability almost every population is relatively distinct from all others. The variability of these populations indicates that the term "ecotype," originally given by Turesson to such populations, is unfortunate. Although the individuals of a given population cluster around a characteristic mean, they do not conform to a definite "type" in the strict sense of this word. For example, plants from Tenaya Lake (2500 m.) when grown at Stanford started flowering between April 17 and June 16, the longest stems varied between 12 and 52 (av. 33.9 ± 1.70) cms., the number of stems per plant between 0.3 and 37.7 (8.80 ± 1.38). Similar variation was shown by all other investigated characters, not only morphological ones as leaf and flower shape, but also physiological ones as degree of winter or summer dormancy, resistance to grazing by rodents, ability to withstand transplanting, and others. This variability is obviously due to at least two causes. One is the drifting in of seeds from adjacent, genetically different populations. The other one is the change of selection pressure (due to changes in the number of predators and competitors, and due to changing weather) from year to year, resulting in a dynamic equilibrium. The genetic variability of these populations prepares them for even rather drastic changes in their environment as well as for the invasion of new niches.

In spite of the variability each population has been severely selected for the climate of its locality. Plants exposed to the incessant winds of the coast line or to the rigorous weather of the higher Sierras have short stems. The alpine plants are winter dormant, while plants from the hot foothills of central California are summer dormant. Under controlled conditions in the greenhouse plants from each population show characteristic response, indicating different requirements in day and night temperature and even of amount of day length in the high altitude populations.

These differences have an obvious selective significance and this has been substantiated by transplanting experiments. Individuals of many populations fail to flower when transferred to the range of another population; they may even die if the climatic differences are extreme. It is immaterial in this connection that in the Californian yarrows there are actually two species, a coastal hexaploid (*borealis*) and an interior tetraploid (*lanulosa*), for the two species are virtually indistinguishable where their ranges meet.

The authors correctly point out that the occurrence of such climatic (or more generally speaking, ecological) races is by no means restricted to plants. The entomological literature is rich in notes on differences (under controlled laboratory conditions!) in regard to hatching time, onset of hibernation or aestivation, number of eggs, etc. in different local races of the same species. It would be worth the effort to gather these scattered notes and review them critically.

The effect of climate and other environmental factors on the genetic constitution of local populations is least conspicuous in the warm-blooded vertebrates which, so to speak, carry their own self-regulated environment with them. But, closer analysis reveals such differences even in mammals and birds, as indicated by the frequency of altitudinal and latitudinal clines, by the geographical variation in clutch size, differences in the beginning of the breeding season (British Starling, White-crowned Spar-

[1] Clausen, J., D. D. Keck, and W. M. Hiesey. 1948. Experimental Studies on the Nature of Species. III. Environmental Responses of Climatic races of Achillea. Carnegie Institution of Washington Publication 581.

row in California), etc. The cold-blooded vertebrates are even more obviously adapted for their local environment, as indicated by the work of Moore on frogs and Heuts and others on fishes.

It is evident from these studies that there is no fundamental difference between plants and animals in the evolution of populations and races that have become adapted to local environments. The difference is one of degree, with insects and plants having much more localized races than birds or mammals. That some of the insect races are as localized as the plant races is indicated by the work of Dobzhansky on *Drosophila pseudoobscura*. None of the insect material, however, can compare with some plant species in the abundance of conspicuous morphological characters in addition to the physiological ones.

The remarkable study of Clausen, Keck, and Hiesey on climatic races in *Achillea* could well serve as a model for similar investigations on other organisms. For, although we believe in the widespread occurrence of genetically different races adapted to local environments, there are actually only few concrete studies available. And, as far as geographically variable morphological characters are concerned (including the subspecific characters of the taxonomist), our ignorance concerning their genetic basis, adaptive significance, and selective value is almost complete. There is a world to be conquered by the biosystematist.

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